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A REPORT ON THE PARASITIC COPEPODA AND BRANCHIURA OF THE FISHES OF LAKE BANGWEULU (NORTHERN RHODESIA)

BY

GEOFFREY FRYER, B.Sc., Ph.D.

*Northern Rhodesia—Nyasaland Joint Fisheries Research Organisation**

[Accepted 10th June 1958]

(With 67 figures in the text)

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INTRODUCTION

Although the fish fauna of Lake Bangweulu and its contiguous swamps is now fairly well known there appears to be no published information on the parasites of these fishes. The present paper attempts to fill this gap in our knowledge insofar as the parasitic crustaceans are concerned by giving an account of the species of this group encountered during a sojourn of more than a year on the shores of the lake, during which time it was possible to examine

* Present address : East African Fisheries Research Organisation, P.O. Box 343, Jinja, Uganda.

several thousand fishes which were fairly representative of the Bangweulu fish fauna.

A general account of the Bangweulu region is given by Debenham (1952) while a briefer account from the standpoint of the hydrobiologist is given by Ricardo (1939) together with a brief account of the fish fauna. The most recent and most comprehensive account of the fishes is given by Ricardo-Bertram (1943).

Most of the parasites studied were collected from fishes caught in the region of Samfya, which lies near the south-western corner of the lake proper, but a number of specimens collected elsewhere in the lake and in the vast Bangweulu Swamps have also been examined.

Type specimens of all the new species described are deposited at the British Museum (Natural History), London.

SYSTEMATIC AND BIOLOGICAL NOTES

The following species have been found during the course of the investigations

COPEPODA

Family Ergasilidae

Ergasilus sarsi Capart

Family Dichelesthiidae

Lamproglena hemprichii Hartmann

Lamproglena monodi Capart

Family Lernaeidae

Lernaea barnimiana (Hartmann)

Lernaea hardingi Fryer

Lernaea laterobrachialis sp. n.

Family incertae sedis

Afrolernaea longicollis Fryer

BRANCHIURA

Family Argulidae

Argulus africanus Thiele

Argulus amblopliites Wilson

Argulus monodi sp. n.

Argulus brachypeltis sp. n.

Dolops ranarum (Stuhlmann)

Chonopeltis schoutedeni Brian

Chonopeltis congicus sp. n.

Each species is dealt with in turn in the following account.

COPEPODA

Family ERGASILIDAE

All the ergasilids collected appear to be referable to a single species which is discussed below.

ERGASILUS SARSI Capart (Figs. 1–7)

The specimens from Lake Bangweulu differ from those of *E. sarsi* described by Capart (1944) from Lake Mweru and the Katanga in their greater size; in the greater length of the egg sacs, and possibly in two minor points of anatomy.

Capart's material, taken from the gills of the cichlid fish *Tylochromis mylodon* Regan, had a total length of only 0·65 mm. The specimens from Lake Bangweulu varied in length as follows :

From *Gnathonemus macrolepidotus* (Peters) (one specimen) 0·856 mm.
From *Synodontis nigromaculatus* Boulenger (two specimens) 1·01 and 1·245 mm.
From *Synodontis nigromaculatus* (in swamps) (one specimen) 1·35 mm.
From *Clarias mellandi* Boulenger (numerous specimens) 1·35–1·53 mm.

These facts suggest that the size of the parasite is influenced by the identity of its host and that size as such is not a specific characteristic.

The egg sacs of the Bangweulu specimens were, irrespective of host, both relatively and absolutely longer than those produced by *E. sarsi* as described by Capart. This again may well be a reflection of the nutritive influence of different hosts and cannot be regarded as a genetical difference.

As for differences in structure, these concern the arrangement of setae on the antennule, some of which arise on the posterior margin of the distal segments as is typical for the genus but which are shown on the anterior margin by Capart, and the presence of a basal seta on leg 5 which is not mentioned by Capart in his description of *E. sarsi*. Little weight can be attached to these points, particularly when it is remembered that Capart's specimens were very small and that preserved specimens of *Ergasilus* are notoriously difficult to observe in detail.

The following remarks are intended to supplement Capart's description and to draw attention to certain points of morphology as observed in the material from Lake Bangweulu.

The anterior limb of the T-shaped marking of the cephalothorax is bifurcated at its tip. This apparently trivial feature may yet prove to be a useful recognition mark.

When the body is distended with eggs the tergites of the body fail to cover the segments to which they belong. In the case of somite five the tergite only covers the anterior half of the somite and gives one the impression that two distinct somites are present.

The mouthparts are not mentioned in the original description so are described briefly here.

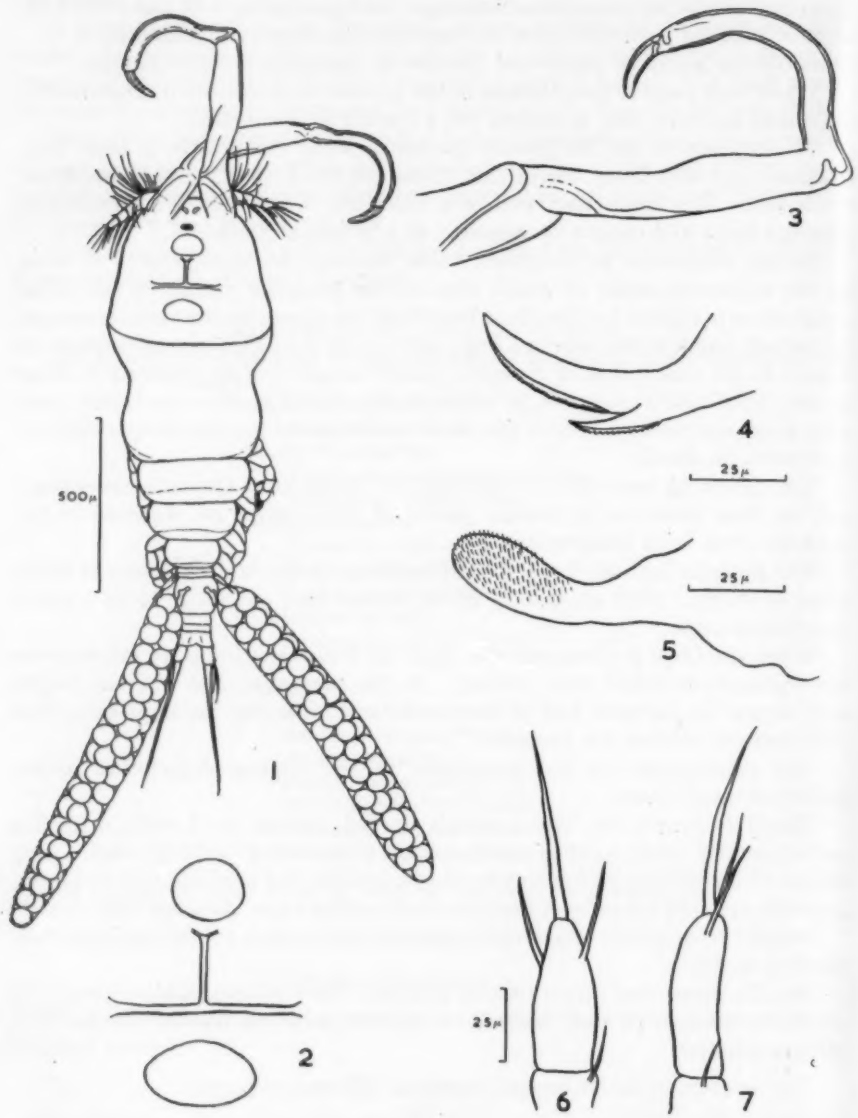
Mandible drawn out into a simple curved cutting tooth with a hyaline and extremely finely toothed membrane on its posterior (cutting) edge. Palp simple, of similar shape to cutting tooth of mandible, but less than half its length, and with a similar but more coarsely toothed cutting edge. Anterior edge smooth.

Maxillule consisting of a simple plate with two simple spines approximately equal in length.

Maxilla drawn out into a bluntly rounded, flattened peg, wider towards its extremity than at its base, and whose anterior surface is densely covered with minute spinules.

The setation of the swimming legs is as follows :—

P1.	Exopod.	1–0	1–1	2–5
	Endopod	0–1	0–1	2–4
P2.	Exopod.	1–0	0–1	0–6
	Endopod	0–1	0–2	1–4
P3.	Exopod.	0–0	0–1	0–6
	Endopod	0–1	0–2	1–4
P4.	Exopod.	0–0	0–5	
	Endopod	0–1	0–2	1–3



Figs. 1–7.—*Ergasilus sarsi* Capart. 1. Adult ♀, dorsal. 2. Sculpture of dorsal surface of cephalothorax. 3. Antenna. 4. Mandible. 5. Maxilla. 6. Leg 5, dorsal. 7. Leg 5, lateral.

Except for leg 4, therefore, the setation is the same as in the closely related *E. macrodactylus* Sars (Note : In the description of *E. macrodactylus* (Fryer, 1956) the formula for leg 2 unfortunately duplicated the endopod setation. That of the exopod is in fact like that described for *E. sarsi*).

Leg 5 is somewhat flattened and differs considerably in appearance when viewed from dorsal and lateral aspects (see Figs. 6 and 7).

Occurrence

As a general rule ergasilids are distinctly uncommon in Lake Bangweulu. Thus during the examination of several thousand fishes only a few specimens of *E. sarsi* have been found on *Synodontis nigromaculatus* Boulenger, both in the lake and in the swamps, and a single specimen has been found on *Gnathonemus macrolepidotus* Peters. Besides these, however, on one occasion several dozen specimens were found attached to the gills of a specimen of *Clarias mellandi* Boulenger. On no other occasion was even a single specimen found on this host. An interpretation of this and allied phenomena in other species, will be presented elsewhere.

Family Dichelesthiidae

Two members of the family Dichelesthiidae, both referable to the genus *Lamproglena*, have been found in Lake Bangweulu. Both are known from inland waters elsewhere in Africa.

LAMPROGLENA MONODI Capart

Syn. *L. nyasae* Fryer.

When describing *L. nyasae* (Fryer, 1956), I was aware of Capart's description of *L. monodi* (Capart, 1944) but felt that my material from Lake Nyasa exhibited sufficient differences to permit the erection of a new species. Since then, however, I have seen specimens from several widely scattered localities, in the Nile, Congo and Zambesi drainage systems (Fryer, 1959) and this, together with information recently published by Capart (1956) who has now studied additional material from the Niger system, has convinced me that all belong to one very variable and widely distributed species.

In Lake Bangweulu a few specimens have been found on the gills of *Tilapia melanopleura* Duméril. In view of its wide host preferences elsewhere—this species seems capable of parasitizing any cichlid genus—it is surprising that it has not been seen on any other cichlid fish in this lake. This applies particularly to *Tylochromis bangwelensis* Regan which is very common there and of which a large number of specimens has been examined.

LAMPROGLENA HEMPRICHII Hartmann

This species, which was already known from the Congo system, was found to occur commonly on the gills of *Hydrocyon lineatus* Bleeker in Lake Bangweulu. Infestations of more than six specimens on a single set of gills are, however, rare.

While strictly quantitative data are lacking the indications are that this species may exhibit seasonal behaviour for, while it was quite common during

the early months of the year, no specimens were seen on several dozen individuals of *H. lineatus* examined from July to November, 1956. They began to appear again after this date. This phenomenon, however, requires more careful checking both in Lake Bangweulu and elsewhere.

Family LERNAEIDAE

Three species of *Lernaea*, one of them previously undescribed, have been found in the Bangweulu region. These are listed below.

LERNAEA BARNIMIANA (Hartmann)

A few individuals of this widely distributed African species have been found on several specimens of *Tilapia melanopleura* Duméril, and three specimens were also found on one of the few examples of *Labeo altivelis* Peters collected in the lake. In all cases the anchor was embedded in the flank of the host.

Considering that it has been recorded from various localities between the lower Nile and Lake Nyasa, including Lake Mweru, its presence in Lake Bangweulu is not unexpected.

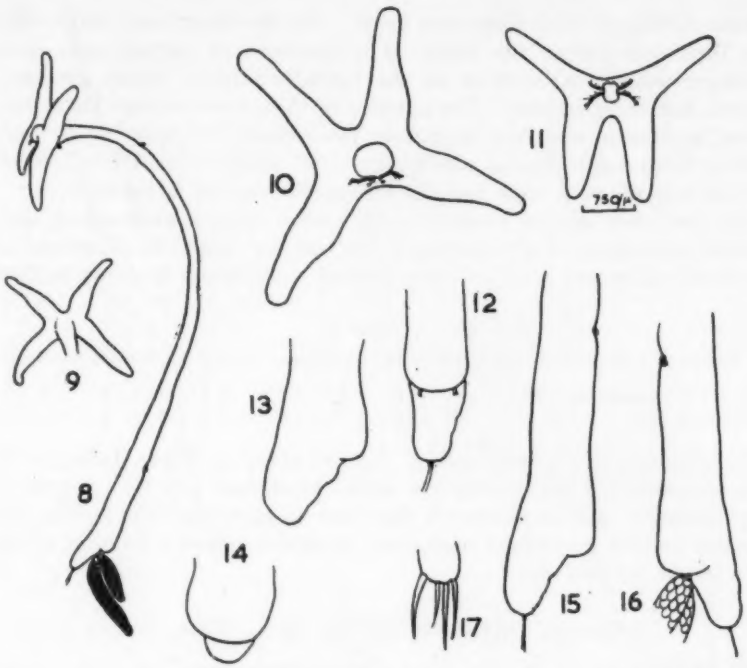
LERNAEA HARDINGI Fryer (Figs. 8–17)

The taxonomy of this species presents some perplexing features, and at present it is extremely difficult to frame a system which will deal satisfactorily with the material so far available.

The material from Lake Bangweulu is very similar in many ways to that of *L. hardingi* from Lake Nyasa, yet had specimens from these two lakes alone been available they would probably have been assigned to separate species on account of certain small but apparently constant morphological differences, and their rather strikingly different preferences both for hosts and for particular regions of the host. However, two complete and three fragmentary specimens collected in Lake Mweru by Mr D. Harding have also been available and these, while having the same host preferences as specimens from Lake Bangweulu, show in some respects greater morphological resemblances to *L. hardingi* from Lake Nyasa than to their counterpart in Lake Bangweulu.

The specimens of *L. hardingi* from Lake Nyasa all have a double pregenital prominence (Harding, 1950 ; Fryer, 1956). In Lake Bangweulu the prominence is simple (Figs. 12–16). In the few specimens from Lake Mweru it is double as in the Nyasan material. The size of the anchor varies in the different populations. Thus, if as a convenient measurement one takes anchor length as the distance between the tips of a pair of diametrically opposed anchor arms, the ratio of body length to anchor length in material from Lakes Nyasa, Bangweulu and Mweru is respectively, approximately 2·0, 3·3–4·0, and 3·0, to 1. In this respect also the material from Lake Mweru is thus less different from the Nyasan material than is that from Lake Bangweulu.

In Lake Nyasa all the specimens were found attached to various parts of the body, but not in the vent region, of cichlid fishes, while in Lake Bangweulu the vast majority of individuals occurred on the non-cichlid fish *Chrysichthys mabusi* Boulenger and almost always occurred around the vent. The few specimens from Lake Mweru all occurred around the vent of specimens of *C. mabusi*.



Figs. 8–17.—*Lernaea hardingi* Fryer. 8. Adult ♀. 9. Anchor of same specimen viewed from below. 10. Head and anchor of another specimen viewed from above. 11. Head and anchor of another specimen viewed from above. 12. Abdomen and pregenital prominence. 13 and 14. Two views of abdomen and pregenital prominence of specimen illustrated in Fig. 8. 15. & 16. Posterior end of body of two other specimens. 17. Leg 5.

It seems certain that all these forms have been derived from a common ancestor and that, isolated as they are in different areas, they exhibit incipient speciation. The logical procedure in dealing with such forms is to regard them as sub-species of a polytypic species, but such treatment, while theoretically sound, has the practical drawback that, apart from the possibility of a slight difference in anchor size which may well be phenotypic, it is scarcely possible to separate specimens from Lakes Mweru and Nyasa on morphological grounds. The considerable variability exhibited by *Lernaea barnimiana* (Hartmann) and *L. cyprinacea* L. should also be borne in mind when considering this problem.

I therefore propose for the time being to regard all these populations as representatives of *L. hardingi* while yet recognising that each appears to be becoming morphologically stable. They are in fact species *in statu nascendi*.

Occurrence and influence of host

As noted above, most specimens were found around the vent of *Chrysichthys mabusi*. Occasional specimens were also found on the flanks of this species, and a very few specimens have been found on *Synodontis nigromaculatus* Boulenger, again usually near the vent. There appear to be no differences

between specimens from these two hosts. On the other hand two specimens have been taken from the flanks of a specimen of *Sargochromis mellandi* Boulenger, which, in contrast to the other two hosts, which are smooth-skinned, is a scaly species. The anchors of these were smaller than those of typical specimens and bore a certain resemblance to those of *L. lophiara* Harding from Lake Nyasa, which indeed is closely related to *L. hardingi*. In other respects they were like the Bangweulu race of *L. hardingi*.

The incidence of this species on its host is readily ascertained, and the degree of infestation of 477 specimens of *C. mabusi* caught in all months of the year except May and June has been studied. The result is shown in Table 1.

TABLE 1

Degree of infestation of 477 specimens of *Chrysichthys mabusi* by *Lernaea hardingi*

Number of parasites per fish	0	1	2	3	4	5	6	7	8
Number in class	376	73	19	4	2	0	1	1	1

As in the case of a related species, *L. bagri* Harding (Fryer, 1956) the higher rates of infestation fall outside the realms of chance, and this, together with other evidence, will be presented elsewhere to show that the larvae of these parasites exhibit gregarious behaviour, a settled parasite tending to attract other larvae to that site.

LERNAEA LATEROBRACHIALIS sp. n. (Figs. 18–25)

Adult female

Length up to at least 2 cm. (allowing for bends).

Head rounded and more or less enclosed by arms of anchor. Anchor with a pair of short, incurved and somewhat bluntly rounded ventral arms and a pair of longer dorsal arms, approximately equally bifid and giving the appearance of two pairs of arms. Dorsal arms directed approximately parallel to anterior portion of body. Anterior branches close set, lying more or less parallel to each other ; posterior branches divergent. Both branches tapered, and each about half as long again as ventral arms.

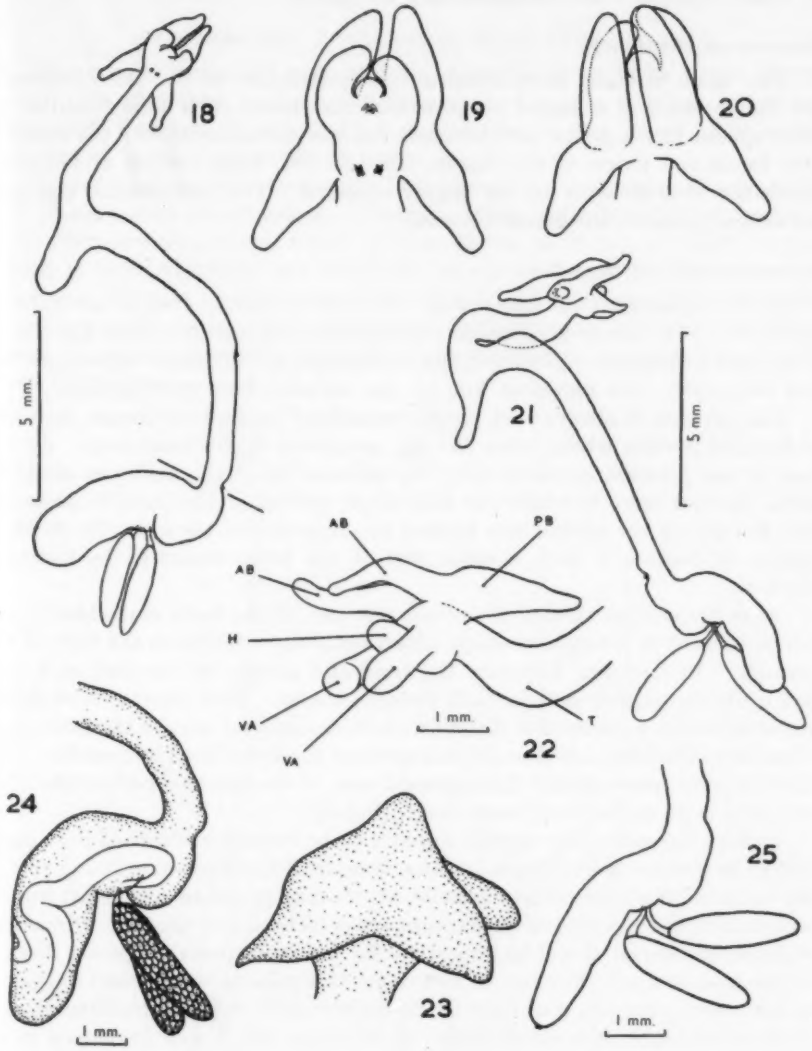
Thorax cylindrical, and bent sharply but by no means regularly anterior to site of second pair of legs (Figs. 18 and 21). Between legs 1 and 2 is a distinct tubular outgrowth twice as long as ventral arm of anchor.

Abdomen long and set at a marked though variable angle to thorax ; swollen in all save smallest specimens (Figs. 18, 21, 24 and 25). Pregenital prominence large and simple ; considerably swollen in large specimens.

Legs located at approximately 4, 30, 54, 72 and 84 per cent of distance along body. Legs 1, 2 and 3 with arrangement of spines and setae as in *L. cyprinacea* and most other species of the genus. Only endopod of leg 4 seen clearly and this also typical in armature.

Egg sacs suspended from body by a distinct membraneous peduncle (Figs. 18, 21, 24 and 25).

Cuticle practically colorless. Gut reddish. Abdomen with whitish patches near tip and with a few similar patches elsewhere. Eggs, both in oviducts and in egg sacs salmon pink.



Figs. 18–25.—*Lernaea laterobrachialis* sp. n. 18. Adult ♀ Holotype. (The whole of that part of the body anterior to the line in the vicinity of leg 4 is buried in the tissues of the host.) 19. Head and anchor of a paratype, ventral. 20. The same, dorsal. 21. Adult ♀, a paratype. 22. Head and anchor of same, lateral. 23. Encapsulated head and anchor as seen when first removed from host. 24. Posterior region showing location of ovaries in abdomen. 25. Posterior region of another specimen.
AB.—anterior branch of dorsal arm. PB.—Posterior branch of dorsal arm. VA.—Ventral arm. H.—Head. T.—Thorax.

Host : *Tilapia macrochir* Boulenger.

Remarks on morphology

The most striking morphological characteristics of *L. laterobrachialis* are the presence of a lateral outgrowth of the thorax such as is found in no other species of the genus, and to which the specific name refers ; the remarkable bends and twists of the thorax, and the very large swollen abdomen to which the ovaries seem to be largely confined. The pedunculate egg sacs are also atypical of the genus *Lernaea*.

Occurrence and effect on host

Several specimens of this species have been found, always on *Tilapia macrochir*. The site of attachment seems to be always either inside the mouth or the gill chambers. Usually a fish, if infected at all, bears either one or, less commonly, two parasites, but on one occasion four were present.

The parasite is always very deeply embedded in the host tissues, only the abdominal portion which bears the egg sacs being visible externally. In the case of one juvenile specimen only the extreme tip of the abdomen could be seen. In two cases in which the abdominal portion of the parasite projected into the mouth the anchor was located in the socket of the eye. In no other species of *Lernaea* is such a large part of the body buried in the tissues of the host.

As is frequent in species of *Lernaea* the part of the body embedded in the fish is encased in a tough envelope which faithfully reproduces the form of the parasite. In addition, however, the head and anchor are encased in a very tough fibrous capsule with a dark metallic colour. This capsule is so firmly attached to the parasite that it appears to be an integral part of the latter and, when first observed, was thought to represent the fused head and anchor. Its effect is to increase greatly the apparent size of the anterior part of the body and give it an entirely different shape (Fig. 23).

In fact, however, the capsule appears to be formed entirely of host tissue and to be cancerous by nature. Quite apart from the interest centring around the cause of this tumour-like capsule, interesting problems are raised in connection with the nutrition of the parasite whilst its head is so encased. Obviously, whilst so enveloped, it will be impossible for the mouthparts to operate directly on the host tissues. Further, in two cases, this capsule was located in the eye socket where absorption of food by diffusion would probably be difficult. As *L. laterobrachialis*, like other species of its genus, has a well developed gut it seems unlikely that food is absorbed through the cuticle which is, in any case, quite tough and thick. How this species manages to obtain sufficient food to maintain itself and produce a continual succession of eggs thus remains a mystery.

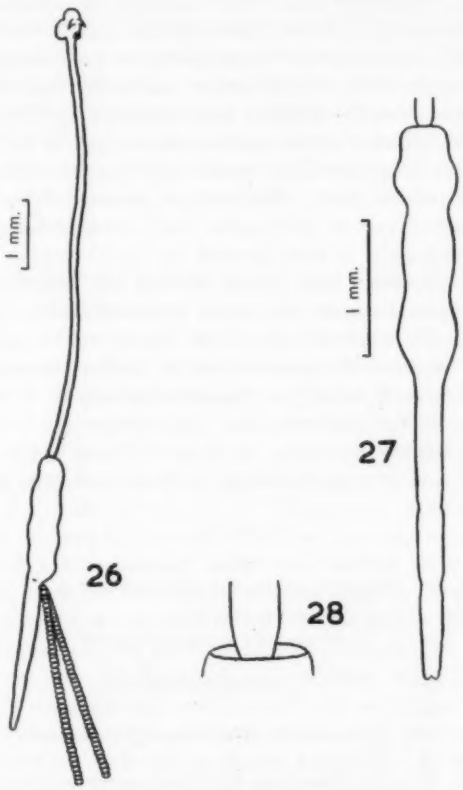
Attention must be drawn to the fact that the host, *T. macrochir*, is one of the species now becoming widely used in fish culture in Africa. A watch should therefore be kept for the appearance of this parasite in ponds as, from its habit of becoming very deeply embedded in the tissues of its host it seems probable that it is one of the most dangerous species of its genus.

Family INCERTAE SEDIS

AFROLERNAEA LONGICOLLIS Fryer (Figs. 26–28)

This species was only very recently described from Lake Nyasa (Fryer, 1956). Its discovery in Lake Bangweulu (and in the Zambesi River and Malagarasi Swamps (Fryer, 1959)) indicates that it may prove to be widely distributed in the freshwaters of Africa.

Most of the few specimens found in Lake Bangweulu occurred on the mormyrid fish *Gnathonemus macrolepidotus* (Peters). These differ from the types taken from *Mormyrus longirostris* Peters in Lake Nyasa in having a " neck " region which is both relatively and absolutely shorter, a longer posterior sac, and colourless cephalic hooks as compared with bright green hooks in the types. Also the posterior sac, while unsegmented, tends, in some specimens, to betray traces of its former segmentation more clearly than is the case in specimens from Lake Nyasa.



Figs. 26–28.—*Afrolernaea longicollis* Fryer. 26. Adult ♀ from *Gnathonemus macrolepidotus* (Peters) in Lake Bangweulu. 27. " Posterior sac ", dorsal. 28. Junction of " neck " and " posterior sac ".

A specimen has also been obtained from *Mormyrops deliciosus* (Leach), but was unfortunately not removed intact so its neck length could not be accurately ascertained. However, it was apparent that this region was much longer than in the specimens from *Gnathonemus*.

The material from the Zambesi (on another mormyrid, *Marcusenius discorhynchus* (Peters)) was intermediate in neck length between that from *Mormyrus* in Lake Nyasa and from *Gnathonemus* in Lake Bangweulu (see Table 2) and the cephalic hooks were green in colour.

Only preserved material (on the gills of *Mormyrops* sp.) was available from the Malagarasi Swamps, and it proved impossible to remove the few available specimens intact, so it was not possible to make an accurate measurement of neck length or to ascertain the colour of the hooks. The proportions of the body, were, however, apparently similar to those of the specimen from *Mormyrops deliciosus* in Lake Bangweulu.

Table 2 indicates the relative lengths of the different regions of the body in specimens from different hosts and different localities. The numerous specimens from *Mormyrus* in Lake Nyasa, of which only two typical measurements are given, were very constant in proportions, but the only two specimens from *Mormyrops* in this lake differed rather markedly from one another.

It is not easy to assess the relative importance of spatial isolation and the influence exerted by different hosts on the morphology of the organism though it would appear that, in general, the neck length is correlated with the length of the gill filaments of the host. Obviously a parasite with a neck as long as that of the specimens found on *Mormyrus longirostris* in Lake Nyasa would be at a great disadvantage if it was located on *Gnathonemus macrolepidotus* of which even large specimens have much shorter gill filaments than have the " average " sized individuals of *Mormyrus* from which the Nyasan specimens were collected. Under such circumstances the posterior sac and part of the extremely slender neck would protrude and be liable to damage or destruction. Contrariwise a short neck would be disadvantageous to an individual settled on *M. longirostris* as the posterior sac, and hence egg strings, would tend to be enveloped by the gill filaments. It is easy to imagine how natural selection could operate here and give rise to distinct species adapted to life on different

TABLE 2

Percentage lengths of the different body regions of specimens of *Afrolernaea longicollis* from different localities and from different hosts

Head	Neck	Posterior Sac	Locality and Host
4	78	18	L. Nyasa (*Mormyrus longirostris*)
4	77	19	,, ,, ,,
4	68	28	,, (*Mormyrops deliciosus*)
3	78·5	18·5	,, ,, ,,
4	71	25	Zambesi R. (*Marcusenius discorhynchus*)
4	70	26	,, ,, ,,
4	59	37	L. Bangweulu (*Gnathonemus macrolepidotus*)
4	60	36	,, ,, ,,
4	56	40	,, ,, ,,
—	70+	26–	,, (*Mormyrops deliciosus*)
—	71+	25–	Malagarasi Swamps (*Mormyrops* sp.)

hosts, but until experimental evidence is produced we have no more grounds for assuming this to be the case than for presuming that the genetical make-up of the parasite is such as to allow it to accommodate itself during development to the situation in which it finds itself. If the latter alternative should prove to be correct, then we have a remarkable case of the environmental control of growth in an arthropod, comparable in some respects with that to be seen in groups such as the corals and sponges.

For the time being I have deemed it advisable to assign all known specimens of *Afrolernaea* to one species, while yet recognising that subsequent work may necessitate subspecific or even specific differentiation.

BRANCHIURA

Family Argulidae

ARGULUS ARFICANUS Thiele

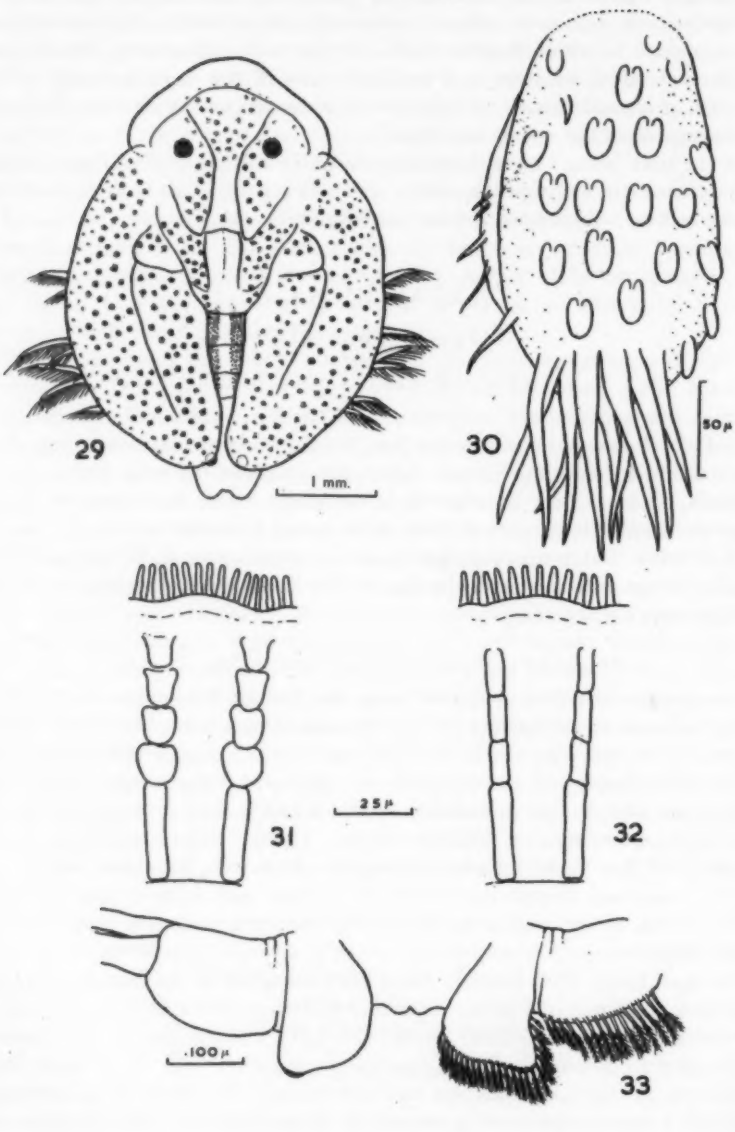
While not particularly common, this widely distributed species is not rare in Lake Bangweulu and in the Bangweulu Swamps. It occurs usually on smooth-skinned fishes but is not rigorously confined to such hosts. In the lake itself, at least near Samfya, it is certainly much less common than is *Dolops ranarum* (Stuhlmann) and the same seems to be the case in the swamps, though I have had numerous specimens from a specimen of *Heterobranchus longifilis* Cuvier and Valenciens, taken in the fairly clear open water of one of the larger swamp lagoons.

ARGULUS AMBLOPLITES Wilson (Figs. 29–35)

This species was first recorded from the Dungu River, one of the north-eastern tributaries of the Congo, by Wilson (1920), who described what he believed to be the two sexes, in each case from a single specimen. When describing a closely related species, *A. jollymani* Fryer, from Lake Nyasa doubts were cast on the association under a single specific name of the male and female described by Wilson (Fryer, 1956). Subsequently I received specimens of this species from Mulungushi Dam, N. Rhodesia, which show that the male and female described by Wilson are indeed not conspecific. Details of this record and a description of the true male are given elsewhere (Fryer, 1959).

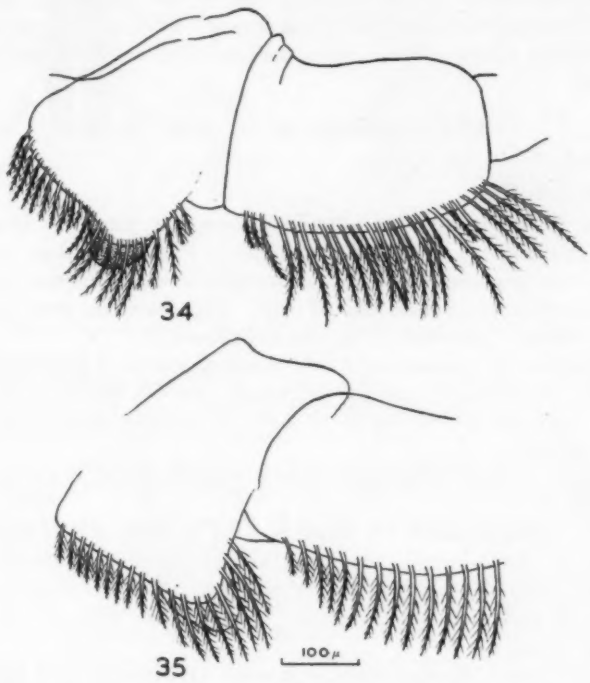
Two specimens, both females, have been obtained in the Bangweulu region, one from a specimen of *Clarias mossambicus* Peters in the lake proper, and the other from *Hydrocyon lineatus* Bleeker in Lake Chaya, one of the lakelets of the Bangweulu Swamps. These specimens, together with those from Mulungushi Dam, permit amplification and amendment of Wilson's description.

Wilson's description and figures of the female indicate that the coxopodite of leg 4 is wedge-shaped and not produced laterally. A casual examination would suggest that my material differs from Wilson's in this respect as this segment is produced laterally and dorsally in the specimens from Lake Bangweulu. The projection, however, which seems to develop more rapidly as the organism increases in size, is not a simple continuation of the segment,



Figs. 29–33.—*Argulus ambloplites* Wilson. 29. Adult ♀, dorsal. 30. Scabrous area of maxilla 31. Ribs of anterior part of sucker. 32. Ribs of posterior part of sucker. 33. Base of fourth pair of legs of ♀.

but a distinct and somewhat chitinised lobe which does not affect the true contour of the somite. The latter is indicated by a fringe of long plumose setæ. Sometimes these setæ almost completely obscure the projection and, was one not aware of its presence, it could easily be overlooked. One has only to compare Fig. 35, which is drawn from a specimen from Mulungushi Dam in which the coxopodite is particularly square cut, with Wilson's figure to appreciate the similarity. The new material is also interesting in showing that the exact form of this segment is rather variable.



Figs. 34–35.—*Argulus ambloplites* Wilson. 34. Coxopodite and basipodite of fourth pair of legs of a ♀ from Lake Bangweulu. 35. The same of a ♀ from Mulungushi Dam.

Wilson describes how the supporting rods of the suckers consist of four elongate pieces. In both the material from Lake Bangweulu and in that from Mulungushi Dam this description is perfectly apt for the posterior rods but not for those of the anterior portion of the sucker which consist of one long rod and four short swollen or vesicular pieces (Figs. 31 and 32).

Wilson refers to the suckers of his specimen as being about one-eighth the "diameter" of the carapace. This description is difficult to understand. In the Bangweulu material the suckers are about 18 and 21 per cent of the maximum carapace width.

What may prove to be a useful diagnostic feature is the presence of a group of spines at the posterior end of the scale-covered scabrous area of the maxilla*. These spines (Fig. 30) are hyaline and not easy to see in preserved specimens.

In the specimen figured one of the scales of the scabrous area was replaced by a small spine, a fact which suggests that the scales are modified spines.

In life the animals are colourless and transparent, the carapace is covered with numerous green blotches of pigment dorsally, and there are two bands of melanophores on the dorsal surface of the thorax covering the uteri. The preserved specimens from Mulungushi Dam were similarly spotted.

A rather interesting fact concerning one of the Bangweulu specimens is that the fish from which it was taken was stunned by dynamite yet the parasite was able to swim quite actively when scraped from its host and placed in a tube of water.

ARGULUS MONODI sp. n. (Figs. 36–44)

Adult female

Length to 5·9 mm.

Carapace broadly elliptical, approximately 1·2 times as long as wide. Cephalic portion fused to thoracic portion. Posterior lobes with bluntly rounded extremities, and extending backwards so as to almost but not quite obscure basal portions of third pair of legs. Gap between posterior carapace lobes very wide so that most of thorax is exposed.

Ventral surface of carapace with five marginal groups of backwardly directed spinules, one at anterior median extremity, one external to antennæ and antennules, and one extending from level of anterior margin of suckers to about level of leg 1.

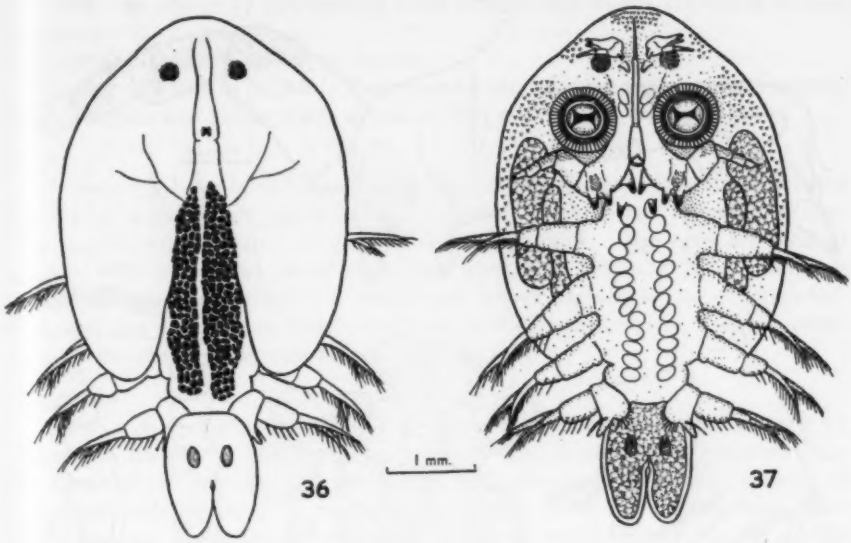
Respiratory surface consisting of two elongate contiguous areas of form shown in Fig. 37.

Abdomen approximately 1·4 times as long as wide and comprising about 24 per cent of total length ; its lobes kidney shaped, tapering posteriorly, and broadly rounded at posterior extremities. Anal incision deep, almost half length of abdomen, and narrow. Furcal rami minute ; situated near base of anal incision.

Eyes fairly small, their centres separated by a distance of approximately one quarter of maximum width of carapace. Median ocellus relatively well developed.

Basal segment of antennule bearing at its posterior corner a stout, fairly long and fairly sharp, heavily chitinized spine directed obliquely inwards and backwards. Terminal segment with a large recurved lateral spine but no anterior or posterior spines. Flagellum just extending beyond distal extremity of lateral spine. Antenna closely associated with antennule. Basal segment with posterior corner somewhat chitinized but not forming a true

* This appendage has very often been referred to as the maxilliped—a name I have used myself —but a consideration of the careful morphological work of Martin (1932), and a study of the larva of *Chonopeltis inermis* in which only one pair of appendages occurs between it and the mandibles, has convinced me that it is indeed the maxilla. The fact that the excretory gland opens on this appendage is also good evidence that it is indeed the maxilla and not the maxilliped.



Figs. 36–37.—*Argulus monodi* sp. n. 36. Adult ♀, dorsal (Holotype). 37. The same, ventral.

spine. Tip of antenna extending beyond tip of antennule. Mesial spine at base of antennule very stout, heavily chitinized and rather bluntly pointed.

" Poison spine " in position typical for genus.

Suckers with diameter rather less than one quarter of maximum width of carapace. Margins " frilly ". Supporting rods of sucker membrane consisting of seven or eight contiguous pieces of which basal is crucible-shaped and the rest spherical to elliptical in shape.

Maxillae typical in general form. Basal segment bearing a long chitinized spine on posterior ventral margin. Second segment bearing two similar spines on posterior ventral margin. Scabrous area pear-shaped and with two slender hyaline spines on posterior margin. Roughened surface of maxillae covered with small ctenoid scales. Located posterior to maxillae is a pair of sternal spines, similar to spines of maxillae.

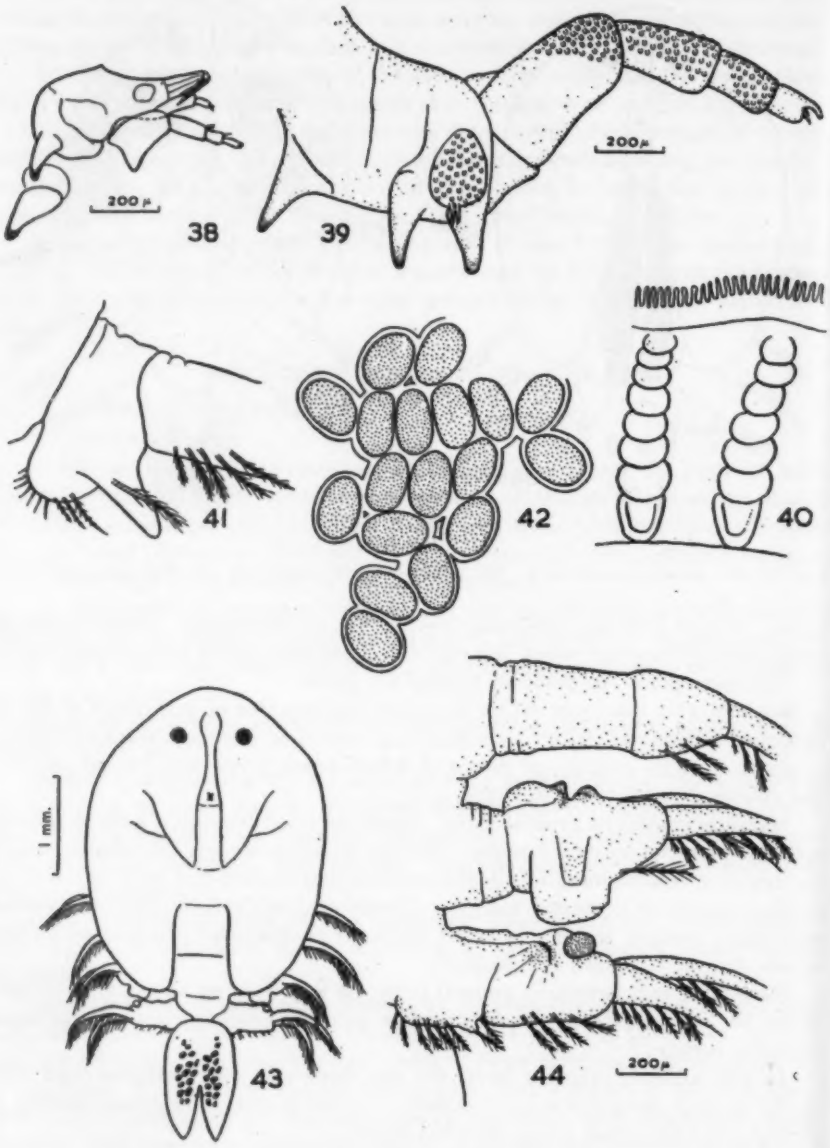
Swimming legs typical in general form: no flagellum on any of legs. Coxopodite of leg 4 produced laterally into a long digitiform process at its outer posterior corner.

In life almost colorless save for the brownish spermathecae and two bands of large irregular shaped masses of black pigment on dorsal surface of thorax overlying uteri. Eggs in uteri white.

Adult male

Length to 4·6 mm.

Carapace of similar shape to that of female, and approximately 1·3 times as long as wide. Posterior lobes partly but not entirely obscuring basal portion of third pair of legs.



Figs. 38–44.—*Argulus monodi* sp. n. 38. Antennule and antenna. 39. Maxilla. 40. Ribs of sucker. 41. Coxopodite of leg 4, ♀. 42. Cluster of eggs. 43. Adult ♂, dorsal. 44. Legs 2, 3 and 4, ♂, ventral.

Abdomen about 27 per cent of total length, and about 1·7 times as long as wide.

Cephalic appendages as in female.

Legs 1 and 2 as in female. Legs 3 and 4 modified by presence of accessory sexual organs and taking form shown in Fig. 44.

Eggs

A few eggs have been deposited in captivity. These, unlike those of most species of *Argulus*, are deposited not in rows but in rather irregular groups. The largest such group contained twenty-seven eggs. The eggs are oval in section with large and small diameters averaging 393 and 260μ. Each is provided with a thick hyaline membrane whose surface is not ornamented. The eggs are white when newly laid but quickly become grey, and the outer hyaline membrane becomes tinged with brown.

Occurrence

Only a few specimens of this species have been collected, always on *Hydrocyon lineatus*. There is some evidence that it exhibits a preference for the bases of the pectoral and pelvic fins. By this means a certain amount of ecological isolation may be maintained between it and *A. brachypeltis* (described below) which infects the same host but which occurs chiefly on the flanks. Both species have been found on a single specimen of *H. lineatus*. Most of the few specimens collected came from the lake proper but one was found in the swamps.

Affinities

This species is closely related to *A. schoutedeni* Monod which is known from the same drainage system, namely from Bukama on the upper reaches of the Lualaba River in the Katanga Province of the Belgian Congo (Monod, 1928), and it is highly probable that the two are derived from a common ancestor. Specific distinction has probably been achieved comparatively recently during a period of isolation in different parts of the same river system. Whether or not this has gone hand in hand with a change of host is not known for the host species of the few known specimens of *A. schoutedeni* is unknown.*

The close relationship of the two species is reflected in similarities in the general form of the body, the presence of only two spines on the basipodite of the maxillae (an unusual feature in the genus *Argulus*), the shape of the coxopodite of leg 4 in the female, the general form of the modification of the legs in the male, and in such minutiae as the ctenoid nature of the scales covering the maxillae.

The differences, however, are quite distinctive and include the well armed antennules and antennæ of *A. monodi*, as opposed to unarmed appendages in *A. schoutedeni*, the longer carapace of *A. monodi* in both sexes, that of

* This specific difference between related species in these two parts of the same river system is not really unexpected, for although the two regions are in direct connection there are effective barriers between them even to fishes as is shown for example by the occurrence in the upper Lualaba or even in waters between the Lualaba and Lake Bangweulu of numerous fishes such as two species of *Protopterus*, four species of *Polypterus*, four species of *Pellonula*, and several others (Poll, 1933), all of which are absent from Lake Bangweulu.

A. schoutedeni covering only the bases of the first two pairs of legs, the absence of a digitiform process on leg 2 and the very much shorter abdomen of the male of *A. monodi*, and the much less crowded nature of the anterior appendages of the new species than those of *A. schoutedeni*.

Remarks

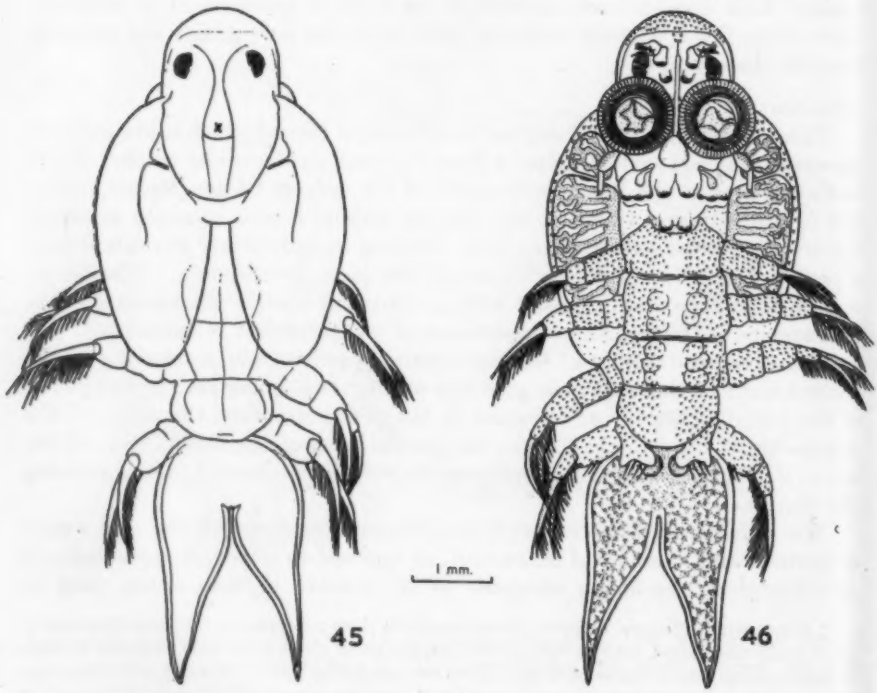
In life this is an active species capable of rapid independent locomotion.

The specific name serves to recognise the contributions made to our knowledge of the parasitic Crustacea of Africa by Prof. Th. Monod.

ARGULUS BRACHYPELTIS sp. n. (Figs. 45–56)

Adult female

Length to 9·9 mm. Carapace small ; about 1·4 times as long as wide. Cephalic portion forming a narrow straight-sided anterior prolongation, bluntly rounded anteriorly, whose width is less than half that of thoracic portion. Posterior lobes of carapace bluntly rounded and reaching back, in larger specimens, only to base of third pair of legs which are only partially covered, and in smaller specimens not quite reaching third pair of legs.



Figs. 45–46.—*Argulus brachypeltis* sp. n. 45. Adult ♀, dorsal (Holotype). 46. Adult ♀, ventral.

Anterior margin of ventral surface of cephalic portion of carapace with a flattened rim covered with fairly stout backwardly directed spinules. Anterior-lateral margins of thoracic portion with a similarly armed rim.

Respiratory surface consisting of a small sub-triangular anterior area and a much larger elongate, more or less parallel sided area.

Abdomen large, longer than wide, and comprising about 37 per cent of total length ; its lobes very broad anteriorly, tapering rather sharply just behind anal incision, and terminating in a rather slender pointed portion.

Anal incision deep. Furcal rami minute ; situated at base of anal incision.

Eye large and well developed, median ocellus fairly well developed.

Basal segment of antennule bearing at its posterior corner a very broad chitinized plate directed obliquely inwards and backwards. Second segment with a minute hook-like anterior spine, a larger hook-like lateral spine and a stout conical posterior spine. Flagellum extending a little beyond distal extremity of lateral spine. Antenna closely associated with antennule. Basal segment with a stout bluntly rounded backwardly-directed conical process. Tip of antenna extending beyond tip of antennule.

Mesial " spine " at base of antennule taking form of a broad heavily chitinized plate.

" Poison spine " in position typical for genus ; long and slender, its tip reaching about to inner margin of rim of cephalic portion of carapace.

Suckers well developed, each with a diameter equal to rather less than a third of maximum width of carapace, and situated very close together.

Maxillae rather small ; typical in general form. Armature of basal segments consisting of broad chitinized plate. (See discussion for details of these and their variation). Swimming legs typical in general form. No flagellum on any leg. Coxopodite of leg 4 produced backwards into a bifid lobe.

Colorless or faintly tinged with brown in places except in dorsal part of thorax. Here are two bands of pigment, consisting of several closely aggregated clumps of melanophores, with a narrow unpigmented band between them.

Male as yet unknown.

Eggs

Eggs have not infrequently been deposited in dishes. Unlike those of most branchiurans they appear always to be deposited singly and not in rows or groups. They are ovoid in section, having axes measuring about $430\mu \times 290\mu$, are grey in colour, are provided with thick membrane, and are sticky when laid. None of those kept in the laboratory ever hatched.

Occurrence

This species has been found only on the tiger fish *Hydrocyon lineatus* Bleeker, and always on the flanks or belly. While by no means common some twenty-five specimens, all females, have been taken from at least ten times that number of fishes collected both in the lake and adjoining swamps. On one occasion four specimens were collected from a single fish, and two have been found twice on a single host, but in most cases a fish carries only one parasite (if any).

This species is not confined to the Bangweulu region as was revealed by a curious set of circumstances. Before I had visited this lake Dr J. P. Harding had sent me a specimen of this species which had been collected swimming free in the River Nile near Khartoum by Dr D. J. Lewis. It was with considerable surprise therefore, that shortly afterwards, I should myself collect the same undescribed species in another part of Africa far removed from that from which the original specimen had come. It is unfortunate that the specimen from the Nile should have been erroneously recorded in the literature as *Chonopeltis inermis* Thiele (Lewis, 1957), a species to which it bears a superficial resemblance.

Remarks

The host, *H. lineatus*, is provided with large stout scales and it seems that *A. brachypeltis* causes it little inconvenience and is indeed probably unable to pierce its armour. It presumably feeds on the mucus which is always present among the scales.

This is an active species capable of swimming quite rapidly. When at rest it cleans its suckers from time to time by flexing its body and wiping them with its anterior legs, much as does *Chonopeltis inermis* (see Fryer, 1956).

The two bands of pigment of the thorax overlie the maturing eggs as they do in several other species so it seems probable that they have a definite function—possibly the protection of the eggs from excessive illumination. The presence of such pigment in the tissues overlying the testes in certain species is additional evidence that this function is to protect the genital products from excessive illumination.

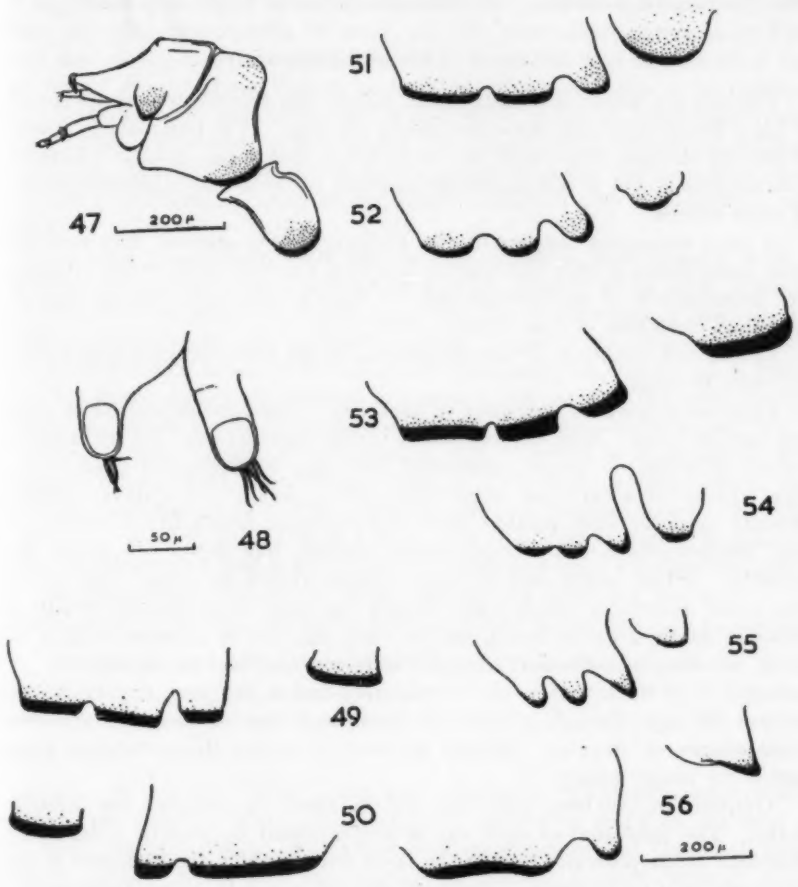
Specimens are difficult to maintain alive after being removed from the host, death usually occurring within twenty-four hours of removal.

A remarkable feature of this species is the apparent absence of males. A preponderence of females in any collection of argulids is not unusual, but in no case with which I am personally acquainted have so many females been found unaccompanied by a single male. This absence, or at least great scarcity, of males indicates the possibility of parthenogenesis. It is a pity that this species is so difficult to keep alive away from its host and that no eggs have as yet been hatched in vitro as these facts indicate that without lavish aquarium facilities the experimental verification of this interesting possibility will be a matter of difficulty.

Variation

In assessing the systematic status of specimens of both the parasitic Copepoda and the Branchiura from different localities one is constantly confronted with the problem of variability and of deciding how much of it is due to the various factors which can influence it. As a contribution to the clarification of this problem the variation of the armature of the maxillae in specimens of *A. brachypeltis* has been considered; advantage being taken of the fact that a good series of specimens, all from the same host species, was available from a single locality. Figs. 49–56 give some idea of this variability.

Some of it is correlated with the size (age) of the specimens, the "teeth" of the maxillæ being narrow and rounded in small specimens and becoming broader and flatter (worn ?) in larger individuals; but there is also some random variation.



Figs. 47–56.—*Argulus brachypeltis* sp. n. 47. Antennule and antenna. 48. Furcal rami. 49–56. Armature of maxilla. 49. Armature of right hand appendage of specimen of length 9·0 mm. 50. Armature of left hand appendage of same individual. 51. Armature of right hand appendage of holotype, length 8·23 mm. 52. The same of a specimen of length 6·5 mm. 53. The same of a specimen of length 9·9 mm. 54. The same of a specimen of length 5·4 mm. 55. The same of a specimen of length 5·4 mm. 56. The same of a specimen from the R. Nile at Khartoum, of length 8·5 mm.

In large specimens there is a tendency for the two outermost teeth to fuse and form a wide plate (Figs. 50 and 56). Such fusion may take place on one maxilliped only of a pair (Figs. 49 and 50). The specimen from Khartoum (Fig. 56) showed such fusion, and until similar specimens had been found in Lake Bangweulu it was thought that this might be indicative of subspecific distinction such as one might reasonably expect in material coming from such widely separated localities. No such distinction is however possible.

DOLOPS RANARUM (Stuhlmann)

This species, which is widespread in Africa, has proved to be quite common in Lake Bangweulu and the surrounding swamps. It is particularly common on smooth-skinned fishes such as *Chrysichthys*, *Eutropius*, *Schilbe*, *Clarias* and *Heterobranchus*, but is not rigorously confined to them and is sometimes found on scaly species.

A very surprising feature of the biology of this species, first noticed in Lake Bangweulu, is that fertilization has been found to involve the production and transference of spermatophores. A note on this phenomenon has been published elsewhere (Fryer, 1958).

The largest specimen of this species which has been collected was a female, 12·5 mm. in length.

Eggs are frequently deposited in captivity. They are deposited in clusters and not in rows. Egg production is quite considerable, for example one female, 10·0 mm. in length, deposited 566 eggs in clusters of from 5 to 121 eggs, except for a very few single eggs, over a period of five days. Eggs are obovate in shape with greatest and least diameter about 612–670μ and 410–446μ respectively and are longitudinally ribbed, five or six ribs being visible dorsally. When newly laid an egg is cream-yellow in colour, but within a few hours darkening takes place though the eggs never become really dark yellow. At the time of laying each is very soft and is invested with a fairly thick covering of adhesive material external to the egg membrane. This material is of thick treacle-like consistency and is not very evenly deposited around the egg, though it does not form such big "blobs" as are seen in some species of *Argulus*. Within an hour of laying this substance hardens and is no longer tacky.

Oviposition has been observed, but detailed observations are difficult to make. The extrusion of each egg is accompanied by violent muscular contractions of the posterior part of the body during which the abdomen is drawn forwards, as if to be drawn away from the egg which has been attached to the substratum.

Unfortunately no eggs have been successfully hatched.

THE GENUS *CHONOPELTIS*: AN INTRODUCTORY NOTE

Collections of fish parasites in Lake Bangweulu have revealed the existence there of two species of *Chonopeltis*. Both of these appear to have been seen before but have been confused both with one another and with *C. inermis* Thiele, the result being a rather chaotic state of affairs. Neither species is

referable to *C. inermis*, both sexes of which have now been adequately described as a result of the finding of abundant material in Lake Nyasa (Fryer, 1956). Both the Bangweulu species were seen by Brian (1940) in material from the lower Congo but he failed to observe their distinctness and gave a composite description, using both species in his illustrations, under the name *C. inermis* var *schoutedeni*. Later Dartevelle (1951) reproduced two of Brian's figures and suggested that the " form " described by Brian was specifically distinct. When reporting the results of work on the crustacean parasites of Lake Nyasa and giving a revised description of *C. inermis* I was able to show that the " form " described and figured by Brian and Dartevelle was indeed distinct from *C. inermis* and suggested that it should be called *C. schoutedeni* Brian (Fryer, 1956). However, at that time I was unaware that Brian had confused two species. It is now necessary therefore to define clearly the species to which the name *C. schoutedeni* must henceforth be attached and to describe a new species.

As Brian's descriptions and illustrations embrace both species, and as Dartevelle figures the male of one species and the female of the other, a purely arbitrary decision must be made regarding the application of the specific epithet *schoutedeni* to one of these species. I therefore propose that the name *C. schoutedeni* be given to the species illustrated in Brian's fig. 4, which is the first figure of the entire animal to appear in his paper. The other species, partially described by Brian, is described as new in the present paper.

Although other species of *Chonopeltis*, one of which is described as new elsewhere (Fryer, 1959), occur in the Congo system, there is no evidence that Brian had other species before him when he prepared his description. Through the kindness of Mr P. L. G. Benoit I have been able to re-examine the material studied by Brian and find it to consist, as suspected from information gained from the Bangweulu collections, of the two species described below.

Each of the following descriptions is shortened by reference to *C. inermis*.

CHONOPELTIS SCHOUTEDENI Brian (Figs. 57 & 59–63)

C. inermis var *schoutedeni* Brian 1940 (Part).
C. inermis var *schoutedeni* Dartevelle 1951 (Part).

Adult female

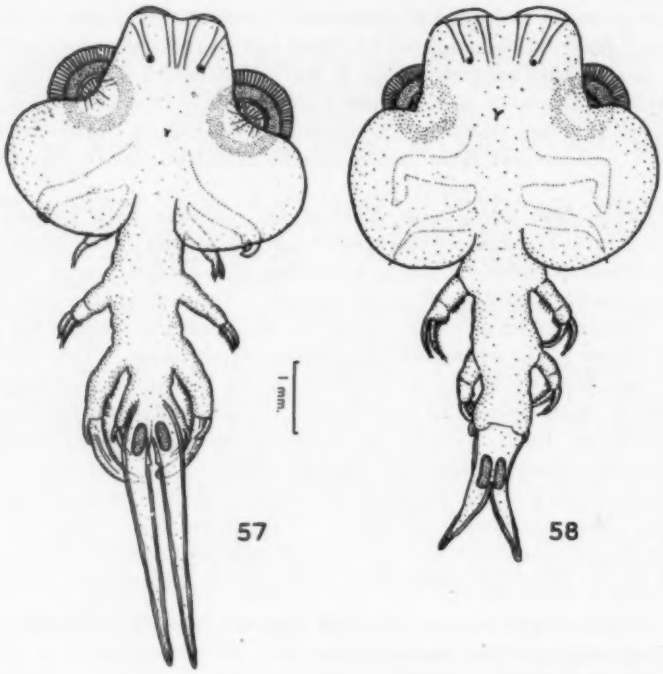
Length to 1·5 cm. Body elongate. Carapace trifoliate ; very short, covering only bases of first pair of legs and occupying some 36 per cent of total body length. Width of anterior lobe of carapace less than half total carapace width. Eyes very small. Ocellus minute, located halfway along carapace. Abdomen consisting of two extremely elongate narrow lobes which comprise some 42 to 43 per cent of total length (49 per cent in a specimen from Lake Mweru). Furcal rami minute, situated near base of abdominal lobes.

Anterior appendages, including suckers, very similar to those of *C. inermis*. Maxilla elongate, of five segments. Basal segment with a chitinous ridge on ventral surface. Second segment elongate, more or less parallel sided and with a chitinous thumb on posterior margin at distal extremity which, by apposition to the three short distal segments, converts the appendage into a prehensile structure.

Leg 1 very small, consisting of a two-segmented sympod with two simple rami of approximately equal length.

Leg 2 similar to leg 1 but larger.

Leg 3 massive and curved like a scimitar, its distal extremity extending back beyond extremity of leg 4 and partly enveloping it. Details of structure as shown in Figs. 57 and 59.



Figs. 57–58.—Adult female of two species of *Chonopeltis*. 57. *C. schoutedeni* Brian. 58. *C. congicus* sp. n.

Leg 4 small and of similar structure to legs 1 and 2, but with markedly unequal rami.

Spermathecae oval in section and situated at base of abdominal lobes.

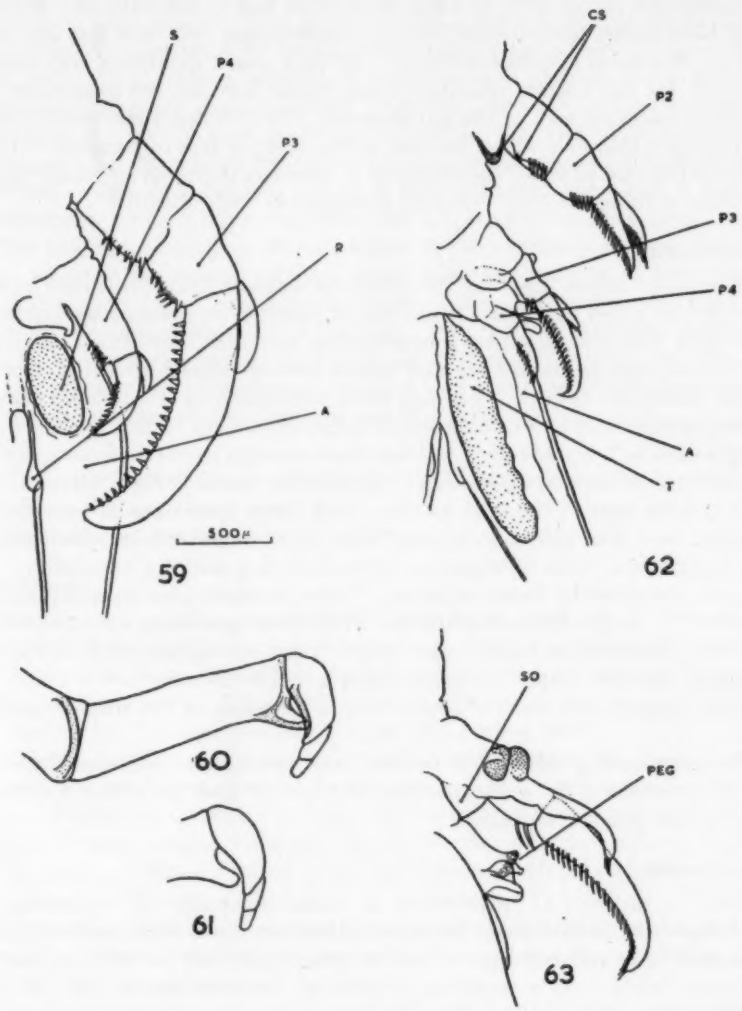
Colour, milk white.

Adult male

Length to 8 mm. General form similar to that of female.

Legs 2, 3 and 4 modified for purposes of copulation. Leg 2 modified only by possession of two chitinized studs on post ventral margin, of which innermost is by far the larger. Legs 3 and 4 greatly modified, having structure shown in Figs. 62 and 63.

Testis sacs elongate and located at base of furcal rami.



Figs. 59–63.—*Chonopeltis schoutedeni* Brian. 59. Region of legs 3 and 4, ♀, ventral. 60. Maxilla 61. Tip of maxilla to show its prehensile nature. 62. Legs 2, 3 and 4, ♂, ventral. 63. Legs 3 and 4, ♂, dorsal.

Legend. A.—Abdomen. T.—Testis. R.—Furcal ramus. P2.—Leg 2, etc. CS.—Chitinized studs on leg 2. S.—Spermatheca. SO.—Socket. PEG.—Peg.

Occurrence

This species occurs both in Lake Bangweulu and in the adjoining swamps. It has been taken fairly commonly on *Gnathonemus* spp. and has also been found on *Mormyrus longirostris* Peters. In each case it exhibits a very marked preference for the narrow chamber which exists between the operculum and the dorsal marginal wall of the gill chamber. Sometimes a specimen is to be found in each chamber whilst the rest of the body is free of parasites. Particularly in the case of small specimens of *G. monteiri* (Günther) it would appear that there is room for only one such specimen in each chamber.

Systematic status

There is no doubt that this species is the same as that illustrated in some of the figures given by Brian (1940), one of which is reproduced by Dartevelle (1951) and that the apparently bewildering structural variations alluded to by Brian are due to his having had before him specimens of this species and of that described below. This has been confirmed by the examination of Brian's material and by examination of seven specimens of this species which, during a visit to Leopoldville, I was fortunate enough to obtain from specimens of *Gnathonemus monteiri* (Günther) captured in Stanley Pool, River Congo, which is quite near to the type locality. All these specimens are constant in structure and are indistinguishable from those collected in abundance in Lake Bangweulu, none of which are subject to any striking variability. The specimen described by Brian as having " lobes caudaux plus ou moins allongés et minces " is assignable to this species, while those specimens whose abdominal lobes were described as being " plus courts " and of which he said " l'abdomen en general est plus trapu ", belong to the new species described below.

Brian's figure of a male is drawn from a specimen of the species described below.

The outstanding differences between the two species concerned are most readily ascertained by a comparison of Figs. 57 and 58 which for ease of reference are printed together.

General habits

Like *C. inermis*, *C. schoutedeni* is quite incapable of swimming. Its appendages are, indeed, even less mobile than are those of its relative. When the animal is at rest the legs are either quite stationary or the first pair may beat very feebly. As a result no respiratory currents are set up. It is not surprising, therefore, to find that the abdominal lobes, through which a brisk circulation of blood takes place, have become much elongated, thus compensating by their increased area for the lack of a current of oxygen-bearing water. Side to side movements of the body cause relatively wide movements of the elongate abdominal lobes, and possibly in part compensate for the loss of a respiratory current. The habit of seeking out a situation on the host near the gills may also be bound up with the lack of a respiratory current.

That the legs of the female are for the most part functionless is indicated by the fact that the blood only appears to circulate to any extent through the third pair.

Locomotion, as in *C. inermis*, consists of "walking" by means of the suckers.

Abortive attempts at mating have been observed between specimens confined in glass dishes. The most surprising feature of this behaviour was that during the process both participants released their hold on the dish with their suckers. If mating takes place on the host in nature—and it is difficult to see how the sexes come together otherwise—and the suckers release their hold, then the adults must be swilled from the fish and must complete the mating process away from the host ; the eggs being deposited on some object elsewhere. This may explain how it is that, although the adult is incapable of swimming, no eggs have ever been seen attached to the host fish.

The attempt at mating, which seemed to be extremely clumsy, lasted for about twenty-five minutes, during which time the male used its prehensile maxillae to grip legs 2 and 3 of the female. The main hold was on leg 3, leg 2 being intermittently grasped and released. The male seemed to be attempting to lie above and parallel to the female but never succeeded in doing so. Throughout the process the only activity observed on the part of the female was a lifting and lowering of the posterior end of the body.

CHONOPELTIS CONGICUS sp. n. (Figs. 58 and 64–67)

C. inermis var *schoutedeni* Brian (1940) (Part)
C. inermis var *schoutedeni* Dartevelle (1951) (Part)

Adult female

Length to 1·12 cm. General form similar to that of *C. inermis* and *C. schoutedeni* but more squat in appearance. Carapace trifoliate ; extending backwards so as to cover the first pair of legs, and occupying some 47 per cent of total body length. Width of anterior lobe of carapace approximately half that of total carapace width. Eyes and ocellus small.

Abdomen consisting of a flat plate, cleft to rather more than half its length into two pointed lobes, the whole comprising some 24 per cent of total body length. Furcal rami minute ; located at bottom of abdominal cleft.

Anterior appendages, including suckers, similar to those of *C. inermis* and *C. schoutedeni*. (But see table below for details.) Maxilla short and stout, not prehensile.

Legs 1 to 3 of similar structure, and each slightly smaller than the preceding appendage. Each consisting of a simple two-segmented sympod and two approximately equal rami.

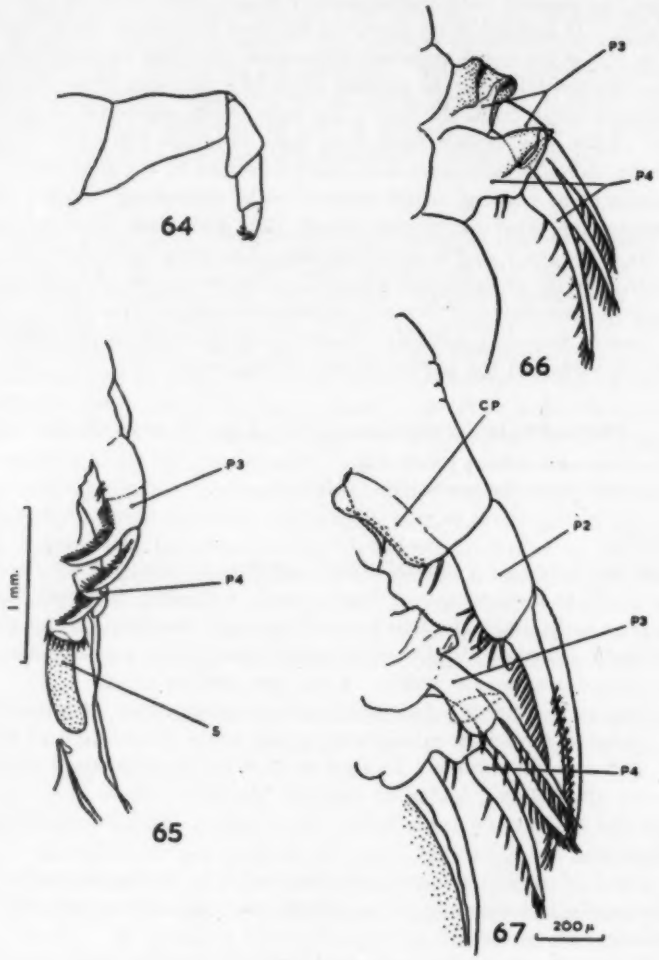
Leg 4 minute, flexed inwards and scarcely visible from dorsal aspect. Endopodite of similar structure to that of preceding appendages. Exopodite very small and swollen.

Spermathecae rather elongate, and situated near base of abdomen.

Colour, milk white to colorless.

Adult male

No males of this species have yet been collected in the Bangweulu region, but several are present in the collection now lodged in the Musée Royal du Congo Belge which was studied by Brian and which has been available to me.



Figs. 64–67.—*Chonopeltis congicus* sp. n. 64. Maxilla ♀. 65. Region of 3 legs and 4, ♀, ventral. 66. Legs 3 and 4, ♂, dorsal. 67. Legs 2, 3 and 4, ♂, ventral. (Figs 66 and 67 drawn from a specimen from the Lower Congo.)

CP. Chitinous plate on leg 2. Other lettering as in Figs. 59–63,

It is convenient, therefore, to describe the male from these specimens, which came from Ango-Ango, near Matadi, in the lower reaches of the Congo.

Length to 8·0 mm. General form similar to that of female. Legs 2, 3 and 4 modified for purposes of copulation. Leg 2 with a broad roughened plate on posterior margin of basal segment. Legs 3 and 4 greatly modified, having structure shown in Figs. 66 and 67.

Abdomen comprising 26 to 29 per cent of total length, and similar to that of female in that its lobes are fused for about 40 per cent of their length. Abdominal lobes attenuated at tips. Furcal rami situated near bottom of abdominal cleft. Testis sacs elongate, extending posteriorly along abdomen beyond point of insertion of furcal rami.

Occurrence

Only five specimens of this species, all of them females, have been collected in Lake Bangweulu. All were found on *Gnathonemus monteiri*, which is also one of the hosts of *C. schoutedeni*. While the data are still scanty the indications are that this species, in Lake Bangweulu at least, exhibits a preference for the flanks while *C. schoutedeni* prefers the wall above the gill chamber as already described. It has not yet been recorded from fishes collected in the Bangweulu Swamps.

General habits

This species, like its relatives, is incapable of swimming. It is, however, a more active species than *C. schoutedeni* with which it has been compared whilst alive. The first pair of legs beat vigorously while the animal is at rest but the other legs are virtually immobile.

Affinities

Structurally this species is much more similar to *C. inermis* than to *C. schoutedeni*. Its separation from the latter species presents no difficulty (compare Figs. 57 and 58) but the differences between it and *C. inermis* are more subtle and are tabulated below for ease of reference.

C. congicus	*C. inermis*
Diameter of sucker about one quarter of carapace width.	Diameter of sucker about one-third of carapace width.
Ribs of anterior lobe of carapace brown in colour.	Ribs of anterior lobe of carapace colorless.
Eyes and ocellus small.	Eyes and ocellus minute.
Rami of leg 2 of ♀ almost equal in length.	Rami of leg 2 of ♀ markedly unequal.
Rami of leg 3 of ♀ almost equal in length, slender and relatively elongate.	Rami of leg 3 of ♀ markedly unequal, short and stumpy.
Leg 4 of ♀ minute, not protruding from body, its rami very dissimilar.	Leg 4 ♀ not minute, protruding, its rami not very dissimilar.
Abdomen of ♀ relatively short, about 24 per cent of total body length.	Abdomen of ♀ relatively long, about 32 per cent of total body length.
In life leg 1 only beats.	In life at least legs 1 and 2 beat.
Leg 2 of ♂ with a broad roughened area posteriorly.	Leg 2 of ♂ with two small roughened studs posteriorly.
Extremities of legs 3 and 4 of ♂ distinctly attenuated.	Extremities of legs 3 and 4 of ♂ not distinctly attenuated.

GEOGRAPHICAL DISTRIBUTION

Lake Bangweulu lies within the Congo drainage area and its fauna is essentially Congolese in character. In addition, however, as was pointed out by Worthington (1933) and Ricardo-Bertram (1943), rather more than half the non-endemic species of fishes (and species so far reported only from this area are very few) are known also from the Zambesi system, thus indicating former connections between the two great river systems. Evidence for the existence of these connections is given also by the distribution of the parasites of the fishes, for several of them are known from both systems, and *Afrolernaea longicollis* and *Lernaea hardingi* which were previously recorded only from the Zambesi system are here recorded from Lake Bangweulu.

From data given by Poll (1933) and David & Poll (1937) it appears that a considerable number of fishes occur in the Upper Congo system just below the lake, viz. in the Lualaba River, Lake Mweru and even in the Luapula River, which, even when recent work is taken into account, have still not been recorded from Lake Bangweulu. It is to the absence of some of these fishes that must be attributed the apparent absence of at least one parasite which from its wide distribution in the Congo system and its occurrence in the Nile and Chad systems might have been expected in Lake Bangweulu. This is *Lernaea haplocephala* (Cunnington) which parasitizes species of *Polypterus*, several of which occur even in the upper reaches of the Congo system, but not in Lake Bangweulu.

The distinctness of the Lualaba-Mweru region from the Bangweulu region is also emphasised by the presence in the former of *Argulus schoutedeni* and in the latter of *A. monodi*—two closely related yet quite distinct species. Also, while negative evidence is to be treated with extreme caution in such cases, it seems remarkable that among the very few specimens of *Chonopeltis* examined from Lake Mweru, three should belong to a species described elsewhere as new (Fryer, 1959) which has not been found in Lake Bangweulu where much more detailed explorations have been carried out.

That connections have existed in the past between the Congo and Nile systems is also borne out by the presence in Lake Bangweulu of species known from both systems, and perhaps most strikingly by the newly described *Argulus brachypeltis* which is known only from Lake Bangweulu and Khartoum.

The investigations in Lake Bangweulu have also emphasised the endemic status of most of the species of *Lernaea* in Lake Nyasa. Of all other lakes in which these parasites might be expected to be found if they existed outside Lake Nyasa, Lakes Bangweulu and Mweru take first place. However, of the seven species previously known only from Lake Nyasa only one has been found in Lake Bangweulu (and also in Lake Mweru). Of the other two species of this genus recorded from Lake Bangweulu one is widely distributed in at least three of the major river systems of Africa and the other is a previously undescribed species whose presence here and apparent absence from the well collected Lake Nyasa further emphasises the endemic status of the Nyasan species.

ACKNOWLEDGMENTS

I am grateful to Mr D. Harding for collecting parasites for me during the course of his work in the Bangweulu Swamps, to Mr P. L. G. Benoit for the loan of specimens from the Musée Royal du Congo Belge and to Dr J. P. Harding for assistance in various ways and for reading the preliminary draft of my manuscript.

SUMMARY

An account is given of the parasitic Copepoda and Branchiura of the fishes of Lake Bangweulu.

At least seven species of parasitic Copepoda and seven species of Branchiura are now known to occur in the lake, one copepod and three branchiurans being described as new in the present paper.

The systematic status of the specimens of *Chonopeltis* previously described from the lower part of the Congo system under the name of *C. inermis* var *schoutedeni* is discussed, and it is shown that two distinct species, neither of them *C. inermis*, were obscured by this name.

Notes on the structure and biology of individual species are given.

The distribution of the species recorded supports and supplements the idea derived from a study of fish distribution that migration has, in the past, been possible between the Congo and Zambezi systems, and also between the Congo and Nile systems, yet at the same time has emphasised the isolation of Lake Nyasa and the endemic nature of some of the species of *Lernaea* recorded from that lake.

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OBSERVATIONS ON THE DISTRIBUTION AND BREEDING OF BRITISH HERMIT CRABS AND THE STONE CRAB (CRUSTACEA : DIOGENIDAE, PAGURIDAE AND LITHODIDAE)

BY

R. B. PIKE

The Marine Station, Millport

AND

D. I. WILLIAMSON

Marine Biological Station, Port Erin

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(With 4 figures in the text)

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INTRODUCTION

During recent years the authors have made extensive collections of adult and larval hermit crabs in the Clyde Sea Area*, round the south of the Isle of Man and in the Channel Islands, while samples and records have also been obtained from other parts of the British Isles. The fullest account of the distribution of hermit crabs in British waters (Selbie, 1921) was found insufficient for obtaining adequate samples of several of the species, and the distribution of some appears to have altered since 1921. Selbie's information on ovigerous females in Irish waters is based on small and infrequent samples. The present records, therefore, should provide a useful addition to the

* Throughout this text, " Firth of Clyde " refers only to the main channel from Glasgow to the Irish Sea. The broader term " Clyde Sea Area " includes all waters bounded by the Kintyre Peninsula on the west, and by the continuation of the mainland coast on the north and east as far south as Loch Ryan (Wigtownshire).

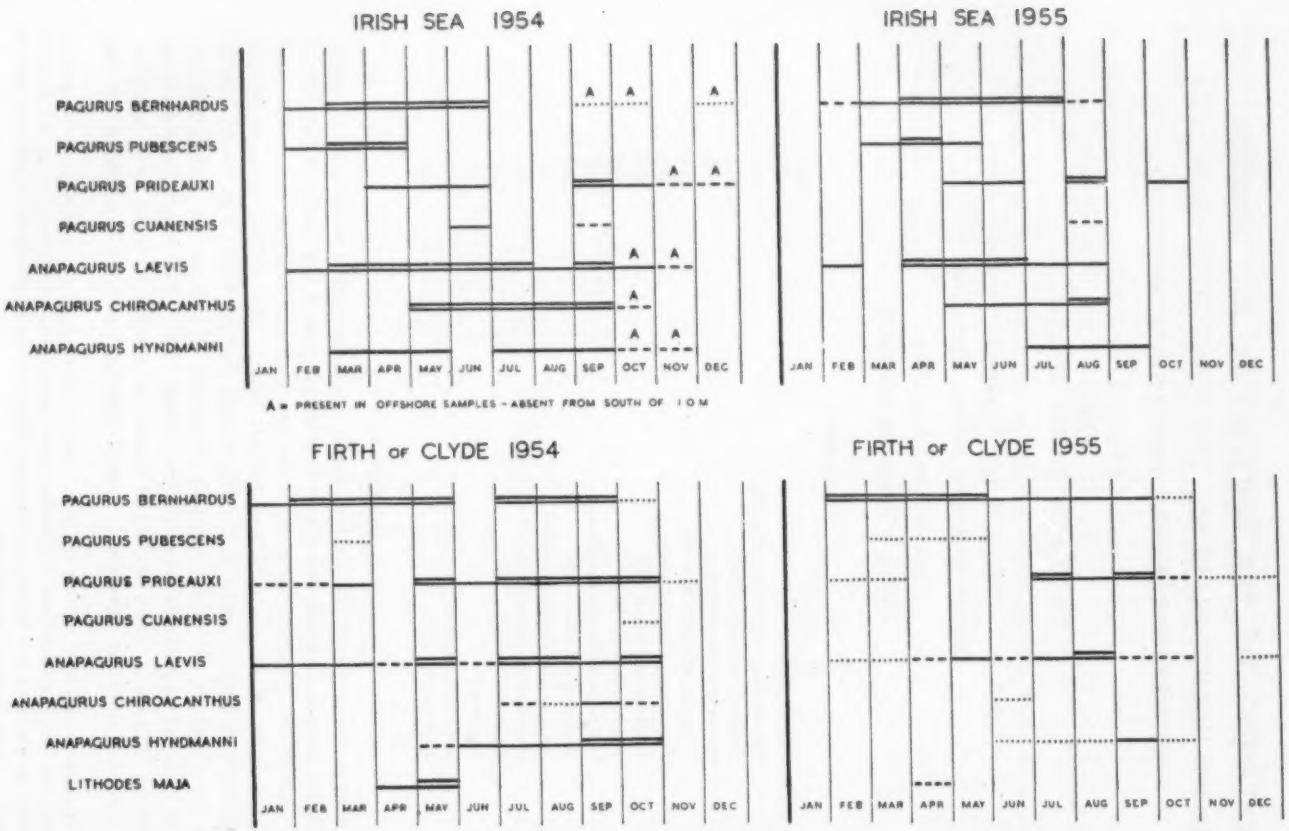

Fig. 1.—Occurrence of larvae in townet samples from the Irish Sea and the Firth of Clyde in 1954 and 1955.

occasional, - - - - - rare, ——— common, ——— very common.

published information on distribution, habitat and breeding. Breeding periods are deduced from periodical observations both on the reproductive state of females and on the occurrence of larvae in the plankton. Descriptions of the larvae are published elsewhere (Macdonald, Pike & Williamson, 1957).

Information collected on the bopyrid parasites of hermit crabs will be given in a separate paper.

TERMINOLOGY AND MEASUREMENTS

The generic name *Pagurus* is used to replace the much better known *Eupagurus* in compliance with the recent decision of the International Commission on Zoological Nomenclature (Opinion 472). Names of several species in current use are those of Thompson (1844) (*Pagurus cuanensis*, *P. hyndmanni* and *P. laevis*). As pointed out by Bell (1844–53, p. 178) these names were published without description or indication, and are therefore *nomina nuda*. Bell described them using Thompson's names. In the case of the last two species, Thompson's specific names may be retained, but the authority for them must be that of Bell. In the case of *P. cuanensis* there is question as to whether Bell's description was published before that of Lucas (1846, as *P. spinimanus*). Forest (1955 and 1956) has established that Lucas' paper was published by 28th March 1846, while Dr H. O. Bull, in a private communication, states that he has incontrovertible evidence that the relevant section in Bell (Part IV ; pp. 145–192 inclusive) was published nominally on 1st January 1846, but actually in December 1845. Thus, on Bull's evidence, *P. cuanensis* Bell must have priority over *P. spinimanus* Lucas and *P. forbesii* Bell over *P. sculptimanus* Lucas. To avoid any confusion in the application of the names used, a reference to an adequate description is given with each species. The names of animals associated with the hermit crabs are those given in the Plymouth Marine Fauna (1957). The developmental stages following the glaucothoe are referred to as " young hermit stages ", these being comparable with the " young crab stages " of the Brachyura (Lebour, 1928). The size of hermit crabs is always expressed as the carapace length, which is the length from the posterior margin of the eye socket to the mid-dorsal point of the posterior margin of the carapace.

DIOGENES PUGILATOR (Roux)

Diogenes pugilator, Selbie, 1921, p. 4, Pl. vi, Figs. 6–9.

Distribution

Selbie (1921) gives records of this species from the British Isles to the Equator, recently Forest (1955) has extended its range south of the Equator to Angola on the west coast of Africa. All past records indicate that it was confined to the South Coasts of England and Wales and probably not plentiful. More recently it was taken by Miss U. Grigg at Llandwyn Island, Anglesey and in 1945 and later (1953–55) it was found to be abundant at Aberffraw, Anglesey (E. W. K.-J.).

On the French coast it has been taken at Trouville and Dunkerque (Bouvier, 1891) and is common near Roscoff (Peréz, 1929).

Fig. 1.—Occurrence of larvae in townet samples from the Irish Sea and the Firth of Clyde in 1954 and 1955.

In the Channel Islands it was not recorded by Sinel (1907), but is now found to be well established in Jersey in St. Aubin's Bay, Ousainé Bay and St. Brelades Bay.

Both the Anglesey and Jersey specimens are of the form with the very slender left cheliped, identified by Bouvier (1891) with the variety *gracilimana* of Miers, and Forest (1955) supports its varietal status within this very variable species.

Habitat and habit

At Aberffraw *D. pugilator* occurs on clean sand subject to considerable wave action. In Jersey the conditions are similar, but the bays are rather more sheltered; in one locality *D. pugilator* has disappeared from an area where some recent silting has taken place, but is present in the unsilted area of the same bay. The species is, however, mentioned by Heller (1863) as occurring in muddy places, and Bouvier records it on both sand and mud. *Diogenes* is most abundant just below low water where it may bury itself in the sand. Apparently the majority of ovigerous females remained just below low water spring tide level, thus avoiding the high and fluctuating temperatures at the water's edge. The males appeared to cover a much greater tidal range, and were frequently found buried in the sand after the tide had receded.

Both in Anglesey and Jersey *D. pugilator* was most frequently found in the shells of *Nassarius reticulatus* (L.) and less commonly in those of *Nucella lapillus* (L.) and species of *Littorina*, especially *L. littoralis* (L.).

Breeding

Of the collection made at Aberffraw, Anglesey, on 2nd June 1954 (Table 1) 65 per cent of the females were without external eggs but with full ovaries. The remaining 35 per cent had eggs in an early stage of development attached to their pleopods. Larvae from these, kept at 13–14°C, hatched on 10th and 11th July. At the time of hatching the brown coloration of maturing ovaries could be seen through the abdominal cuticle of the these females, indicating a second brood of eggs to follow. This second brood was confirmed by the collection of larvae from the plankton in late August and September.

In collections from Jersey made on 19th August 1955 (Table 1) 36 per cent of the females had ripening ovaries in addition to well developed external eggs probably representing the first brood, and 56 per cent had empty ovaries and external eggs without eye pigmentation. The great majority of this latter group were probably carrying their second brood. The remaining 8 per cent were without eggs and with empty ovaries; these might have hatched eggs before the sampling period.

The breeding periods and habits of *D. pugilator* are probably similar in Anglesey and the Channel Islands. In both areas ovigerous females are likely to occur from June until September and larvae from July until October.

The eggs measure c. 0.4×0.2 mm. when approaching maturity, and are smaller and more elliptical than in other species of hermit-crab considered. The number carried ranges from about 790 at 4 mm. to 1400 at 6 mm. carapace length, and is much higher than in specimens of *Pagurus* or *Anapagurus* of comparable size.

TABLE 1

Details of samples of *Diogenes pugilator* in 1954 and 1955. (*) denotes majority with mature ovaries.

	2 June 1954 Aberffraw, Anglesey 0–3 m. below low water (spring tide)	12 July 1955 St. Brelades B., Jersey, C.I. low water (neap tide)	19 Aug. 1955 St. Aubins B., Jersey, C.I. low water (spring tide)	19 Aug. 1955 St. Aubins B., Jersey, C.I. ¼–1 m. below low water (spring tide)
Total males	86	91	53	13
Total females	77	11	48	66
Females without eggs	50*	0	7	2
Females with eggs without eye pigmentation	27	8	18	46
Females with eggs with eye pigmentation	0	3*	23*	18*

PAGURUS BERNHARDUS (L.)

Eupagurus bernhardus, Selbie, 1921, p. 15, Pl. i, Figs. 1–11.

Distribution

This species is found from the Mediterranean northwards as far as Iceland and the Murman Sea. It is exceedingly plentiful on all coasts of Great Britain, Ireland and the Channel Islands. (Selbie, 1921 ; Bouvier, 1940).

Small specimens, of carapace length up to 12 mm., are very abundant between tide marks in spring and summer, less so in autumn and winter, and are only occasionally found in deep water (70–100 m.). The majority appear to spend their first spring and summer between tidemarks, and to migrate offshore during the autumn.

In intertidal and shallow water collections most of the specimens have been found in the shells of *Littorina littorea* (L.), *Nucella lapillus* (L.), *L. littoralis* (L.), and *Nassarius reticulatus* (L.), in that order of preference. In sub-littoral collections from about 40 m. of water, small hermit crabs usually occupied the shells of *Turritella communis* Risso and *Gibbula tumida* (Montagu). Practically all specimens of over 15 mm. carapace length, from all areas and depths, have inhabited the shells of *Buccinum* or *Neptunea*. Associations with other animals have been noted. The sponge *Suberites domuncula* (Olivi) is much less frequently associated with *P. bernhardus* than with either *P. pubescens* or *P. cuanensis*. The anemone *Calliactis parasitica* (Couch) is a common associate on the south coast and in the Channel Islands, but is not found in the Irish Sea or in the Clyde Sea Area. *Hydractinia echinata* (Fleming) is common on inhabited shells from sub-littoral collections, especially in the Clyde Sea Area. *Nereis fucata* (Savigny) is also found more commonly below

tide marks, and in the Clyde Sea Area this increases from 3 to 5 per cent in shells collected from 5 m. depth to 20 per cent in shells from 40–80 m. The barnacle *Alcippe lampas* Hancock was found only below tide levels ; at Fairlie in the Firth of Clyde 7 per cent of shells were infected at 5 m. depth, and only 2 per cent at 40–80 m.

Breeding and growth

The incubation period of the eggs is probably similar to that of *P. pubescens* under the same conditions. It probably extends over more than three months in winter and spring, and rather less in summer and autumn.

In the Clyde Sea Area ovigerous females were present in all samples except those taken in October and November, and were most common in winter and early spring (Fig. 2). Most of the eggs were in a late stage of development (with eye pigment) in March and April 1954 and from February to May 1955. None of the ovigerous females showed developing ovaries, so that successive broods must be well separated and the majority of females probably have only one brood in the year. Larvae were most abundant in the spring, but they may be present in any month from January to September (Fig. 1). Although it was difficult to rear larvae in the laboratory, those which did survive indicate that at about 15°C. each of the four larval stages may last from five to fourteen days, the glaucothoe stage from nine to nineteen days and each of the early young hermit stages from sixteen to thirty-nine days. The carapace length is 1·5–1·8 mm. in the first young hermit stage and increases by from 0·1–0·4 mm. at each moult. There is considerable difference both in the frequency of moult and in the growth at each moult even between specimens kept under apparently identical conditions. None have been reared beyond the fifth young hermit stage. In the early young stages the pleopods are of the male type and disposition (described by Jackson, 1913) except that the first young hermit stage usually retains vestiges of the additional pleopods present in the glaucothoe (described by Macdonald, Pike & Williamson, 1957). The smallest specimen seen with the female number of pleopods had a carapace length of 2·8 mm., but the additional anterior pleopod was small and the others were still of the male type. Another specimen of carapace length 3 mm. (probably less than six months old) had 101 eggs and all pleopods of the female type. The great majority of females of carapace length over 4 mm. are ovigerous in the early spring. The size of the egg increases from c. $0{\cdot}56 \times 0{\cdot}5$ mm. when freshly laid to c. $0{\cdot}8 \times 0{\cdot}73$ mm. before hatching. The eggs are considerably smaller than most other species of *Pagurus* and the numbers range from 750 at 7 mm. to 48,000 at 26 mm. carapace length. This number is high when compared with other species of *Pagurus*.

Samples of specimens probably one year old, taken from 5 m. depth off Great Cumbrae, Firth of Clyde and intertidally from the Isle of Man had an overall carapace length of 9 and 8 mm. respectively. In each region the sexes were the same size and females were about twice as common as males. Owing to the long breeding period and the variation in growth rate, it is not possible to estimate the age of larger individuals. The largest recorded, over 30 mm. carapace size, are likely to be at least three years old.

EGGS WITH EYE PIGMENT
EGGS WITHOUT EYE PIGMENT
WITHOUT EGGS
80

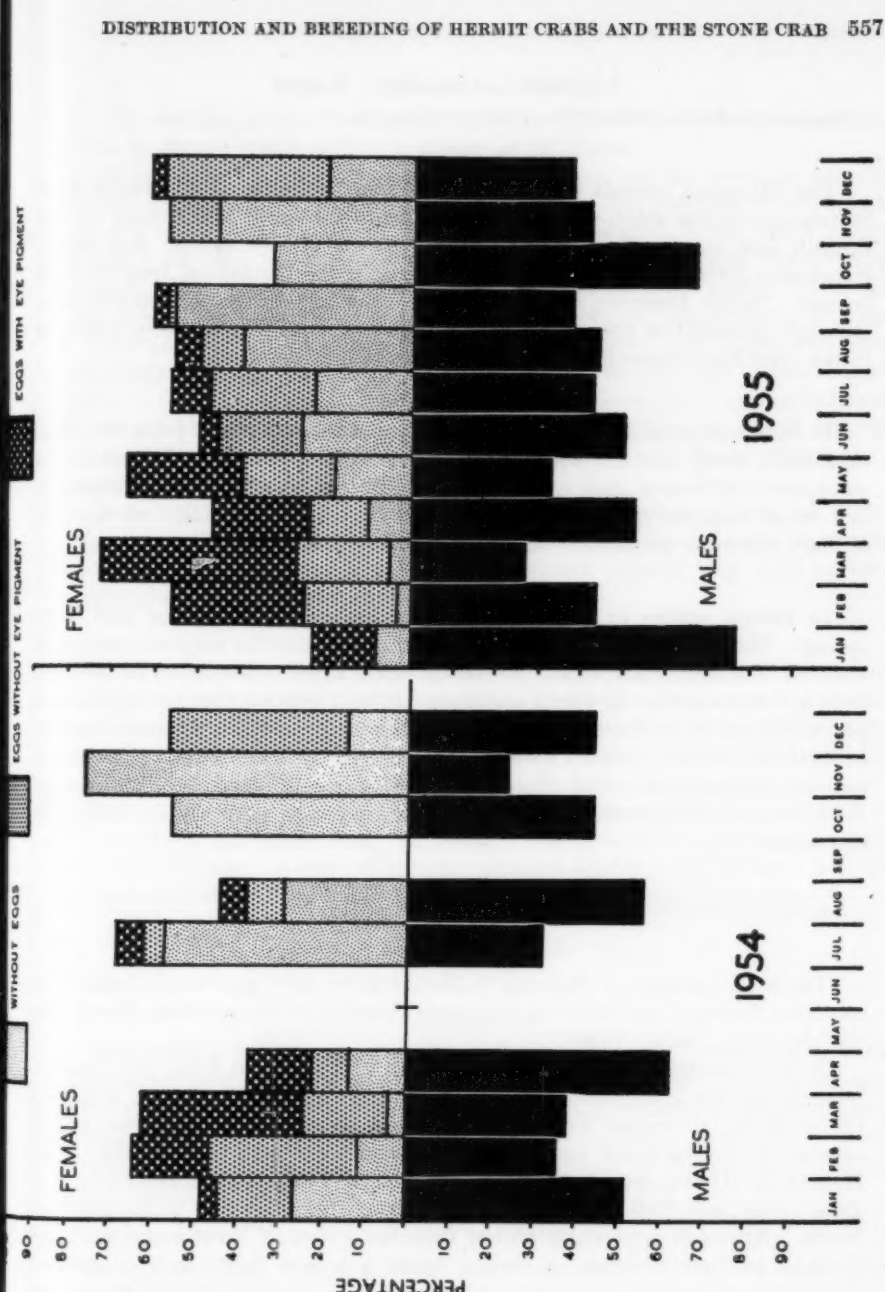

Fig. 2.—Sex ratio and reproductive state of females in samples of *Pagurus bernhardus* from the Firth of Clyde in 1954 and 1955.

PAGURUS PUBESCENS Krøyer

Eupagurus pubescens, Selbie, 1921, p. 29, Pl. ii, Figs. 4-7.

Distribution

The European records of this species given by Selbie (1921) range from Spitzbergen to the south-west of Ireland and as far south as Durham on the English east coast. More recent British records do not extend this range. Henderson (1886 b) records it as common within the Clyde Sea Area on hard ground. Today, however, it appears to be rather scarcer throughout the area, although plentiful in the neighbouring Sound of Jura. It is fairly common in the Irish Sea, especially off the south-east of the Isle of Man.

Habitat and habit

In the Clyde area this crab is usually obtained at a depth of from 10–30 m. on a clean sandy bottom, whereas in the Isle of Man it is most frequent on a substratum of broken shell and stones at a depth of 30–40 m. It is frequently associated with the sponge *Suberites domuncula* (Olivi), especially off the Isle of Man, where 90 per cent of the crabs were invested with it.

Breeding

In British waters ovigerous females are found only in winter and early spring. This restriction of breeding to the colder months may be correlated with the northern distribution of the species. From observation on females kept in the laboratory at about sea temperature, it appears that the incubation period is just over three months. Larvae were considerably more common in the Irish Sea than in the Clyde Sea Area in both 1954 and 1955, and occurred between February and May (Fig. 1). The size of egg is about the same as in *P. bernhardus*, but insufficient females carrying eggs were obtained to give egg counts.

PAGURUS PRIDEAUXI Leach

Eupagurus prideauxii, Selbie, 1921, p. 34, Pl. ii, Figs. 1–3.

Distribution

There are records of *Pagurus prideauxi* from the Cape Verde Islands to southern Norway, but none for Denmark, Sweden or the southern North Sea (Selbie, 1921 ; Balss, 1926).

It is moderately common, but nowhere abundant, in both the Channel Islands and the Plymouth area. It is common at Redwharf Bay, Anglesey (E. W. K-J.), all round the Isle of Man and in the Clyde Sea Area, but it appears to become much less common in western Scotland north of the Clyde. Henderson (1886a) recorded it from the Shetland Isles and Moray Firth, and Balss (1926) and Bull (personal communication) have found it in the Firth of Forth. Although apparently absent from the coasts of Northumberland and Durham in 1909 (Norman & Brady, 1909) it is now fairly well established there and appears to have moved south during the last twenty-four years (H.O.B.).

Selbie (1921) records *P. prideauxi* as being rare on the north coast and plentiful on all other coasts of Ireland.

Habitat and habit

This species prefers clean sandy bottoms in 20–30 m., but it is sometimes found in deeper water and on a variety of substrata.

Of well over 2,000 specimens examined, all have had the anemone *Adamsia palliata* (Bohadsch) on, or enveloping, the shell. The anemone is not able to live and reach sexual maturity without *Pagurus prideauxi*, but under experimental conditions the hermit crab can live indefinitely without the anemone (Berner, 1953). After attaining a carapace length of about 8 mm. the hermit crab does not normally change its shell ; the growth of the anemone provides it with an ever extending cloak. Shells of *Littorina* and *Natica* are most commonly used in the Clyde area, but in the Irish Sea and the Channel Islands shells of *Gibbula magus* (L.) and *Turritella communis* Risso are as frequent. In many cases the shell covered by the *Adamsia* is partly decomposed, suggesting that the anemone extracts calcium from it. *Nereis fucata* (Savigny) is sometimes found within the shell.

Periodical collections from the west of Great Cumbrae, Firth of Clyde, suggest that during most of the year individuals of this species are fairly evenly spread over a wide area, but during the winter months they tend to form aggregations in the deeper water.

Breeding

In the Clyde Sea Area and the Isle of Man some ovigerous females and larvae are found all the year round (Figs. 1 and 3). Ovigerous females are least common in November, and the larvae develop most successfully in the autumn. Most females have two, and a few possibly three, broods in the year (cf. Brandis, 1897 ; Bott, 1940 for the Mediterranean).

The size of egg increases from c. $0{\cdot}75 \times 0{\cdot}65$ mm. when new laid to c. $0{\cdot}90 \times 0{\cdot}73$ mm. when ready to hatch. The number of eggs carried ranges from 370 at 8 mm. to 6000 at 18 mm. carapace length ; this is about half the number carried by *Pagurus bernhardus* of comparable carapace lengths.

PAGURUS CUANENSIS Bell, 1846

Eupagurus cuanensis, Selbie, 1921, p. 26, Pl. iv, Figs. 1–3.

Distribution

This species extends from southern Norway into the North Sea at least as far south as Northumberland (Selbie, 1921 ; Balss, 1926). It is uncommon in the Clyde Sea Area and in the Irish Sea, but it is common at Morfa Bychan, Portmadoc, North Wales (E.W.K.-J.) and very plentiful in Jersey, Channel Islands. It extends southwards through the equator to Angola and Sebastian Bay in South Africa (Forest, 1955).

Habitat and habit

It is found from near low water down to a depth of at least 80 m. The substratum varies from mud and muddy stones (Salcombe, Jersey, Isle of Man) to clean gravel (Salcombe, Clyde).

The majority of the shells of specimens taken by Allen & Todd (1900) and many of those taken by Selbie (1921) were covered by the sponge *Suberites*

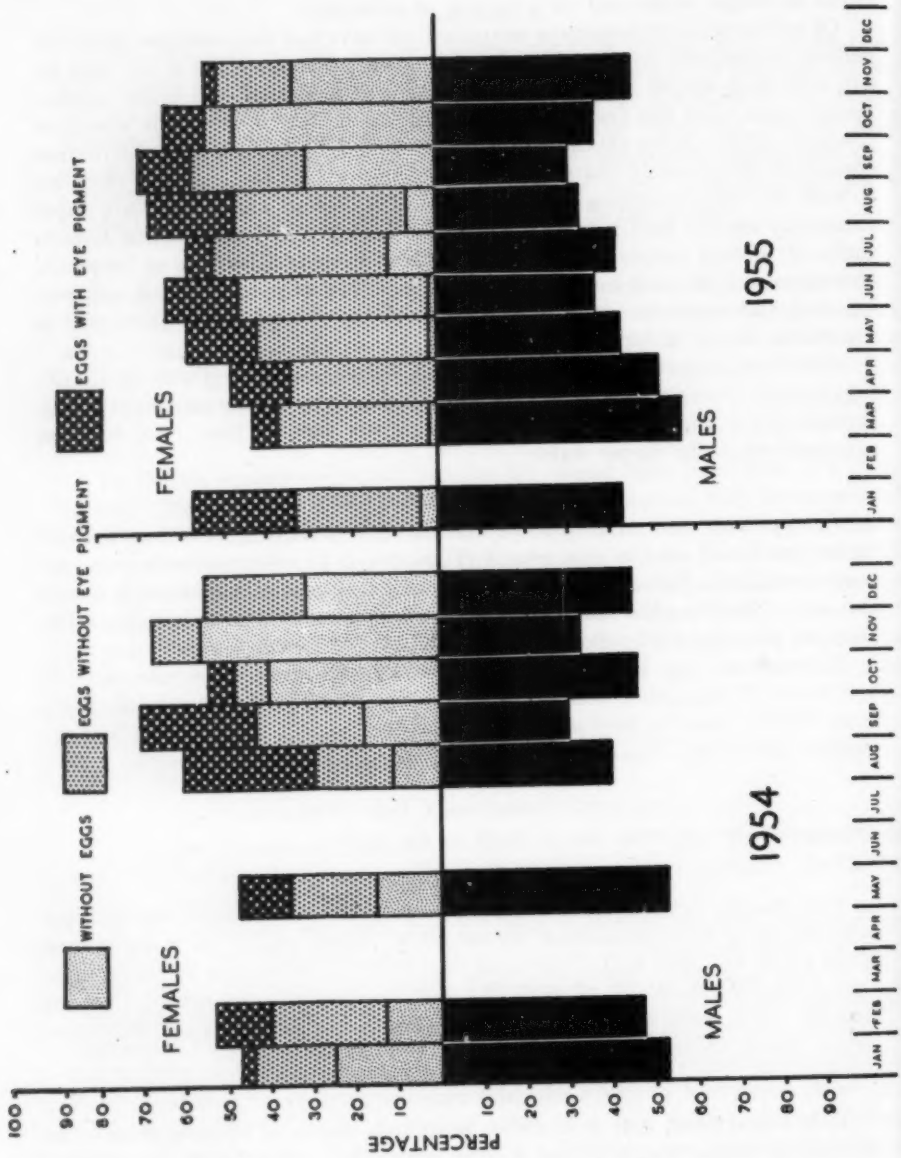

Fig. 3.—Sex ratio and reproductive state of females in samples of *Pagurus prideaux* from the Firth of Clyde in 1954 and 1955.

domuncula (Olivi), but the sponge occurred on only about 5 per cent of specimens from the Irish Sea or the Clyde Sea Area and on none from Jersey. In Jersey the crab usually occupies the shells of *Nucella* or *Nassarius*, while at Portmadoc (E.W.K.-J.) and in the Firth of Forth (Scott, 1905) it favours *Turritella*. In the Clyde Sea Area *Aporrhais pes-pelecani* (L.) is almost invariably chosen, and off the Isle of Man, where the average size is appreciably larger, about 80 per cent inhabit the shells of *Colus gracilis* (da Costa) with most of the remainder in *Ocenebra erinacea* (L.).

In the small samples obtained from the Clyde Sea Area and off the Isle of Man the sexes have been present in about equal numbers, but in intertidal collections from Jersey the males have considerably outnumbered the females. (See Table 2).

TABLE 2

Details of samples of *Pagurus cuanensis* from Elizabeth Castle, Jersey, Channel Islands.

	20 July 1955 low water (spring tide)	20 Aug. 1955 low water (spring tide)
Total males	71	105
Total females	46	26
Females without eggs	10	16
Females with eggs without eye pigmentation	28	8
Females with eggs with eye pigmentation	8*	2

(*) denotes majority with mature ovaries.

Breeding

Ovigerous females are first found in March (Selbie, 1921; Plymouth Marine Fauna, 1957) and a second brood occurs in the autumn (Table 2). First stage larvae were fairly common in June 1954 in the Irish Sea (Fig. 1), but later stages were always rare. All stages were common in Jersey in August 1955.

Although larvae of *P. cuanensis* are appreciably smaller than those of *P. prideauxi* (see Macdonald, Pike & Williamson, 1957), they hatch from eggs of similar size (c. $0{\cdot}9 \times 0{\cdot}7$ mm.) and the numbers range from 200 at 4 mm. to 285 at 6 mm. carapace length. *P. cuanensis* is the smallest species of *Pagurus* here considered and its reproductive capacity is the lowest.

PAGURUS FORBESII Bell, 1846

Eupagurus sculptimanus, Selbie, 1921, p. 19, Pl. v, Figs. 4–8.

Distribution

This species is recorded from Cape Verde and Senegal (Forest, 1955) to near Aran Island on the west of Ireland (Selbie, 1921). Although it has not been taken off the French Channel coast, nor from the Channel Islands, there are a number of records for the south coast of England (Marine Biological Association, 1957).

Fig. 3.—Sex ratio and reproductive state of females in samples of *Pagurus prideauxi* from the Firth of Clyde in 1954 and 1955.

Breeding

A single larva which may belong to this species was taken off Plymouth on 4th October 1955 (Macdonald, Pike & Williamson, 1957).

CATAPAGUROIDES TIMIDUS (Roux)

Catapaguroides timidus, Bouvier, 1940, p. 143, Pl. iv. Figs. 12–13.

Distribution

This species has been recorded from Angola to Roscoff (Bouvier, 1940). One female, without eggs, was taken by Mr P. G. Corbin off Plymouth in 1955 (Marine Biological Association U.K., 1956), and two small males were taken by us off Great Cumbrae, Firth of Clyde, in 1956 and 1957. No larvae have been taken by us in British waters.

ANAPAGURUS LAEVIS (Bell)

Anapagurus laevis, Selbie, 1921, p. 44, Pl. vii, Figs. 7–9 ; Pl. viii, Figs. 1–3.

Distribution

A. laevis is found in southern Norway, in the Faeroes, and plentifully off all coasts of Great Britain and Ireland except from the southern North Sea area. It has been recorded only once from the Channel Islands (Norman, 1907) and appears to be rare off the French channel coast. Forest (1955) extends its southern limit from Senegal to just south of the equator on the West African coast and probably as far as the Cape of Good Hope.

Habitat and habit

The species occurs on clean sand and gravel, but is most abundant on muddy sand. The great majority of those seen have occupied the shells of *Turritella communis* Risso along with small specimens of *Nereis fucata* (Savigny), and this confirms observations by Allen & Todd (1900) at Salcombe.

Breeding and growth

As in *P. bernhardus*, the pleopods in all specimens in early young stages resemble those of the adult male in type and disposition. The external *vas deferens*, on the coxa of the left fifth leg of the male, appears in rudimentary form at a carapace length of 2·0–2·3 mm., probably corresponding to the fourth or fifth young stage. It becomes fully formed in two more moults, at a carapace length of 2·9–3·3 mm. Females may develop the pleopod on the second abdominal segment at a carapace length of 2·4 mm., when they may also show developing ovaries. Specimens may reach a carapace length of 8 mm., but no reliable estimate of their age can be made.

Ovigerous females and larvae occur throughout most of the year (Figs. 1 and 4), so that females probably hatch at least two broods. The glaucothoe and later zoeal stages are most plentiful in the autumn samples.

The size of the fresh egg is c. 0·5 × 0·45 mm. and increases to c. 0·75 × 0·6 mm. when ready to hatch. The number of eggs carried is only about half that of *Diogenes* of equivalent size, but considerably higher than in other species of *Anapagurus* of comparable size : 219 at 3 mm. to 825 at 7 mm. carapace length.

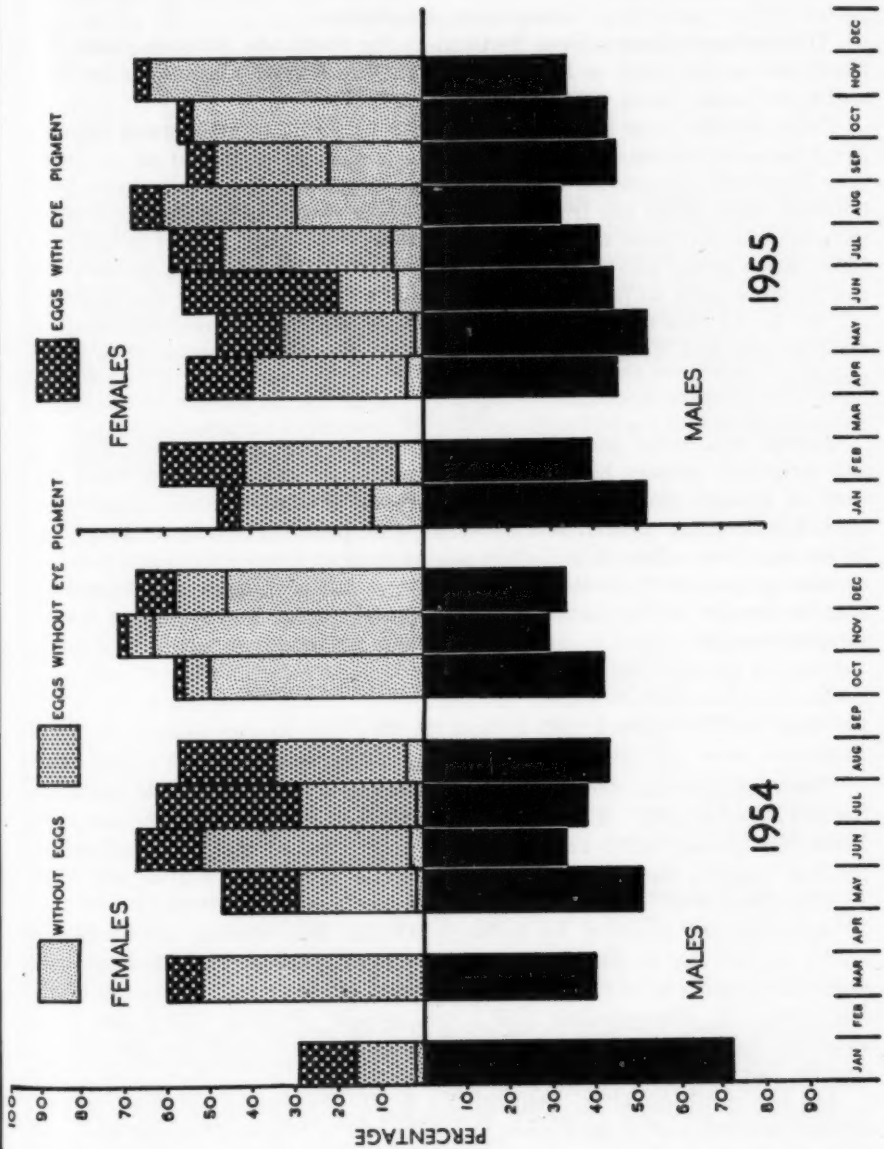

Fig. 4.—Sex ratio and reproductive state of females in samples of *Anapagurus laevis* from the Firth of Clyde in 1954 and 1955.

ANAPAGURUS HYNDMANNI (Bell)

Anapagurus hyndmanni, Selbie, 1921, p. 49, Pl. viii, Figs. 4–7.

Distribution and habitat

This species is known from Portugal to the Shetlands, extending into the North Sea as far south as Durham and into the English Channel as far east as Pas de Calais (Balss, 1926 ; Bouvier, 1940).

It is plentiful near low water and down to about 18 m. in most bays in the Channels Islands (Sinel, 1907). It is almost as abundant as *A. laevis* near Plymouth (Plymouth Marine Fauna, 1957), but few adults have been obtained from either the Irish Sea or the Clyde Sea Area, and most of those recorded are from sand or gravel. The larvae are not uncommon in either of these latter areas, and it seems probable that better collecting grounds for the adults remain to be discovered. Unpublished records exist for Anglesey (E. W. K.-J.), the Orkneys (Mr W. M. Thompson, record communicated by Mr Rendall) and Northumberland (H.O.B.). In the last region it is fairly common.

Breeding

Larvae can occur from March to November (Irish Sea, 1954 ; Fig. 1), and ovigerous females have been taken in March and September from the west of Ireland (Selbie, 1921). The species therefore appears to have an extended breeding period, and most females probably hatch at least two broods in a year. The egg is slightly smaller than in *A. laevis* (c. $0{\cdot}48 \times 0{\cdot}4$ mm. increasing to c. $0{\cdot}69 \times 0{\cdot}54$ mm.), and the number of eggs is considerably less for females of the same size : twenty-eight at 2 mm. to 156 at 4 mm. carapace length.

ANAPAGURUS CHIROACANTHUS (Lilljeborg)

Anapagurus chiroacanthus, Bouvier, 1940, p. 148, Fig. 102.

Distribution and habitat

The range of this species is from Cap Bojador (West Africa) to southern Norway (Forest, 1955 ; Bouvier, 1940). It is not recorded from the southern North Sea (Balss, 1926), and there is no recent record for Northumberland. Dr Bull suggests that in the record of Norman & Brady (1909) it may have been confused with *A. hyndmanni* which is not included by them.

Although not recorded by Selbie (1921) for Irish waters nor by Moore (1937) for the Isle of Man, it has recently been taken in gravelly situations round the south end of the Isle of Man and in similar situations in the Clyde Sea Area. *A. chiroacanthus* (Lill.) var *gracilis* (Fenizia, 1937) has been identified by Dr Bull and Dr R. Desai in collections from both the Isle of Man and the Isle of Muck on the west coast of Scotland.

On the south coast of England Mr J. D. Macdonald obtained several specimens south west of the Plymouth breakwater in 1934 and Norman recorded it for Guernsey in 1861 but not in 1907.

Most specimens from off the Isle of Man have been in *Nassarius* shells, with larger specimens (carapace length 3–4 mm.) in shells of *Gibbula tumida* (Montagu).

Breeding

The presence of larvae from May to October (Irish Sea, 1954, Fig. 1) suggests two broods in a year. Few ovigerous females have been collected, but the eggs are of about the same size as in *Anapagurus hyndmanni* (c. 0·65 × 0·55 mm. when mature) and seem to be produced in comparable numbers.

LITHODES MAJA (L.)

Lithodes maia, Selbie, 1921, p. 56, Pl. ix, Figs. 1–4.

Distribution and habitat

Lithodes maja has been reported from Spitzbergen to Holland and Belgium, but not from the English Channel nor south of Yorkshire on the English east coast (Selbie, 1921 ; Balss, 1926). Its continued presence off the Northumberland coast is confirmed by Dr H. O. Bull. Irish records are for the south coast (Thompson, 1844), off County Wexford (Bell, 1844-53) and on the Porcupine Bank (Selbie, 1921). Two undated nineteenth century records for the Irish Sea are included by Moore (1937), but no precise localities are given, and there are no recent records for this area. It is fairly common in parts of the Clyde Sea Area, particularly off Tarbert, Loch Fyne (100–150 m.) and to the west of Inchmarnock Island (80–100 m.).

Breeding

Eggs are laid in the autumn (September to November) in the Clyde area, and are carried throughout the winter months. The larvae are liberated in April or May and the parent moults soon afterwards in preparation for a second brood. From specimens observed in the aquarium it appears that during the period of the moult and until the time of egg laying a male is in attendance on the female, in much the same way as for *Pagurus bernhardus* and *P. prideauxi* (Bott, 1940). The male and female stand facing each other, the male holding one of the walking legs of the female. Males show an immediate interest when a " soft " female is placed in the same aquarium tank, and they may dispute for possession of the female. It appears that the presence of a freshly moulted female can be detected some distance away.

Larvae were taken in the Firth of Clyde in April and May 1954 and April 1955 (Fig. 1).

The eggs are very large (c. 2·0 × 1·8 mm. when mature) and give rise to comparatively advanced larvae (Macdonald, Pike & Williamson, 1957). No egg counts have been made.

SUMMARY

The observations concern the British species of *Diogenes*, *Pagurus*, *Catapaguroides*, *Anapagurus* and *Lithodes*. Their distributions are summarized, and in the case of *Diogenes pugilator* and *Pagurus prideauxi* there is some evidence of change in distribution during the present century. Habitats and localities where the species are common are described.

Breeding periods, particularly in the Firth of Clyde and the Irish Sea, are deduced from the occurrence of ovigerous females and of larvae. Observations are made on the size and number of eggs in each species.

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FEEDING IN THE PEDUNCULATE CIRRIPEDE *POLLICIPES POLYMERUS* J. B. SOWERBY

BY

H. BARNES* AND E. S. REESE

The Marine Station, Millport, Scotland, The Department of Zoology, University of California, Los Angeles and the Friday Harbor Laboratories, University of Washington, Seattle

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(With 2 plates and 8 figures in the text)

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INTRODUCTION

The rhythmic cirral activity of many barnacles is well known ; in addition to providing a mechanism for the capture of food, the simultaneous movements of the body serve a respiratory function by driving a current of water through the mantle cavity. Water is taken in anteriorly and forced out over the back of the cirral net ; such movements also serve to take nauplii out of the mantle cavity expelling them over the back of the cirri with the exhalent jet (Barnes, 1955). These rhythmic movements may be observed in most genera of the Cirripedia, both pedunculate and operculate, although the form of the activity may be modified by current speed (see, for example, Southward, 1955). The genus *Pollicipes*† appears to be exceptional.

It is readily seen by watching *P. polymerus*, either in the laboratory or on the shore, that there is no rhythmic extension and retraction of the cirral net. The behaviour is similar to that described for *P. spinosus* by Batham (1945)

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† Accepting Darwin's (1851) reasoning, the generic name *Pollicipes* will be used rather than *Mitella* which, however, following Pilsbry (1916) is more commonly employed in the United States of America.

who, observing that when the animal is covered with water the cirri are extended and make occasional twitching and incurling movements, came to the conclusion that the cirral net acts only as a filtering device, the collection of food depending more on the effect of the surrounding water than on movements of the cirri. Examination of gut contents showed that although other material was present small crustaceans formed the bulk of the diet.

FIELD OBSERVATIONS

P. polymerus occurs on the Pacific coast of America southwards to Baja California, being limited largely to the mid and lower tidal zones. It is particularly abundant in exposed rocky situations and indeed, as Batham observed for *P. spinosus*, is usually absent from quiet bays or sheltered places. Commonly, the species occurs in clusters—often dense—attached directly to the rock, to *Mytilus californianus*, and to other sedentary animals particularly barnacles or their shelly remains. Solitary animals are rare. As the tide rises and water reaches the animals the cirri are slowly extended and retracted as each wave passes over them. Later the cirri are not usually completely withdrawn between successive waves but hang limply out from the opening. More prolonged wave action and wetting leads to full extension of the cirri with the sack held wide open and the body raised in the mantle cavity. When the flow of water is moderate, or when the animals are constantly submerged, a single cirrus or the whole cirral net may be rapidly contracted without withdrawal into the mantle cavity.

STRUCTURE OF THE CIRRI AND MOUTH PARTS

The general structure and arrangement of these parts is remarkably similar throughout the whole family ; variations are, however, used by systematists to characterize species. In spite of this, and the fact that the efficiency of the cirral net as a captorial device has often been stressed, little attention has been given to the functional significance of its morphology, particularly that of the groups of spines. Darwin (1851) and Nussbaum (1890) have described the anatomy of *P. polymerus*.

Cirri IV–VI are very similar ; each consists of some 16 to 21 laterally flattened segments, protuberant on their anterior faces (see Fig. 1 for nomenclature). The two rami are equal in length. Each segment bears a series of stout and often serrated spines (usually six) arising laterally from the protuberance and directed laterally (Fig. 2b–d, A–F). These spines form a graded series so that they decrease in length from the distal to the proximal part of the segment (Fig. 2a & b). The shorter proximal spines (D, E. F), point downwards and touch or overlap the long distal spines (A) of the next segment (Fig. 2a). Within this group of stout spines and on the crown of the protuberance is a dense cluster of smaller spines (G), both smooth and serrated, and these curve towards the distal portion of the ramus. In addition, the distal margin of the anterio-lateral face of each segment bears a tuft of small spines (H), more abundant on the outer than the inner side of the ramus, together with a further group of similar small spines (I) on its posterior distal margin (Fig. 2). The spines on the segments of the pedicels form pad-like

groups (Fig. 6), one group on the distal and two on each proximal segment and on Cirrus IV these pedicelar groups tend to be quite distinct. The most proximal spines on each first segment tend to form a border that anteriorly leads to the more specialized groups (described below) on the anterior cirri.

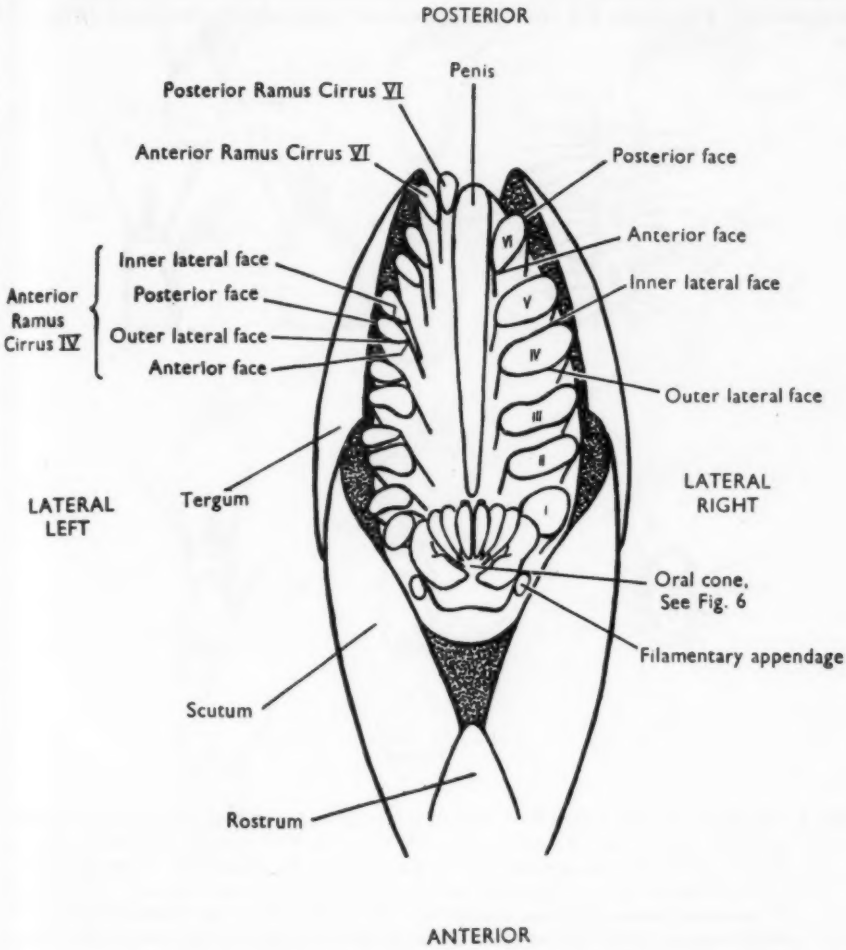

Fig. 1.—Diagram of ventral view of *P. polymerus* to indicate nomenclature used ; cirri on right side cut across the pedicel, cirri on left side cut across the rami.

The posterior rami of Cirri II and III have fewer segments but otherwise are similar to those of Cirri IV–VI : however, it must be noted that the anterio-lateral group (Fig. 2e, H) has more numerous spines which extend further to the posterior on the distal margin. Moreover, the stout spines themselves (Fig. 2e, A–F) are asymmetrically arranged ; those on the outer margin are

straighter and point more directly to the anterior, while those on the inner margin are curved and point more to the side. The distal segments of the anterior rami of Cirri II and III are similar and, except for a reversal of the asymmetry referred to above, resemble the segments of the posterior rami (Fig. 2f). The proximal segments are highly modified and must be dealt with separately. On Cirrus III the three proximal segments are involved (Fig. 3)

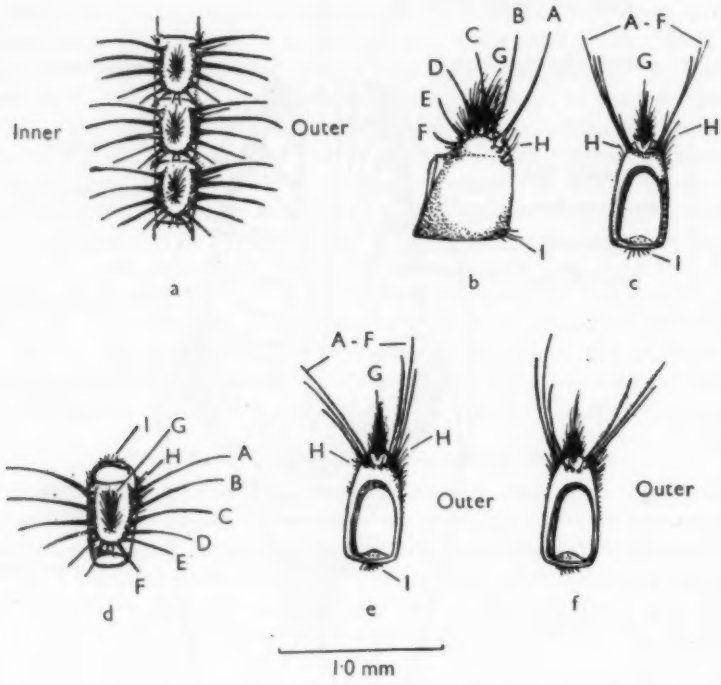

Fig. 2.—Segments of rami of Cirri IV, V and VI (a–d) and segments of distal portion of anterior rami of II and III and of posterior rami of Cirri II and III (e–f). (a) Anterior view of three segments showing arrangement of spines ; note the apposition of lateral spines. (b) Outer lateral view. (c) Proximal view. (d) Anterior view single segment. (e) Segment of posterior ramus of Cirrus II and III. (Proximal view). (f) Proximal view of a distal segment of anterior ramus of Cirrus II and III ; note the reversal of asymmetry. (For lettering, see text).

and these will be considered first. All three basal segments have brush-like pads composed of variously modified spines set on the protuberance which is itself somewhat asymmetrical. On the most distal segment of these three, the spines on the outer lateral margin (Fig. 3, Cirrus III, A–F) of the group are strong and analogous (if not homologous) to the major spines (Fig. 2, A–F) of the posterior cirri ; they point in an anterior direction. Inwards from these

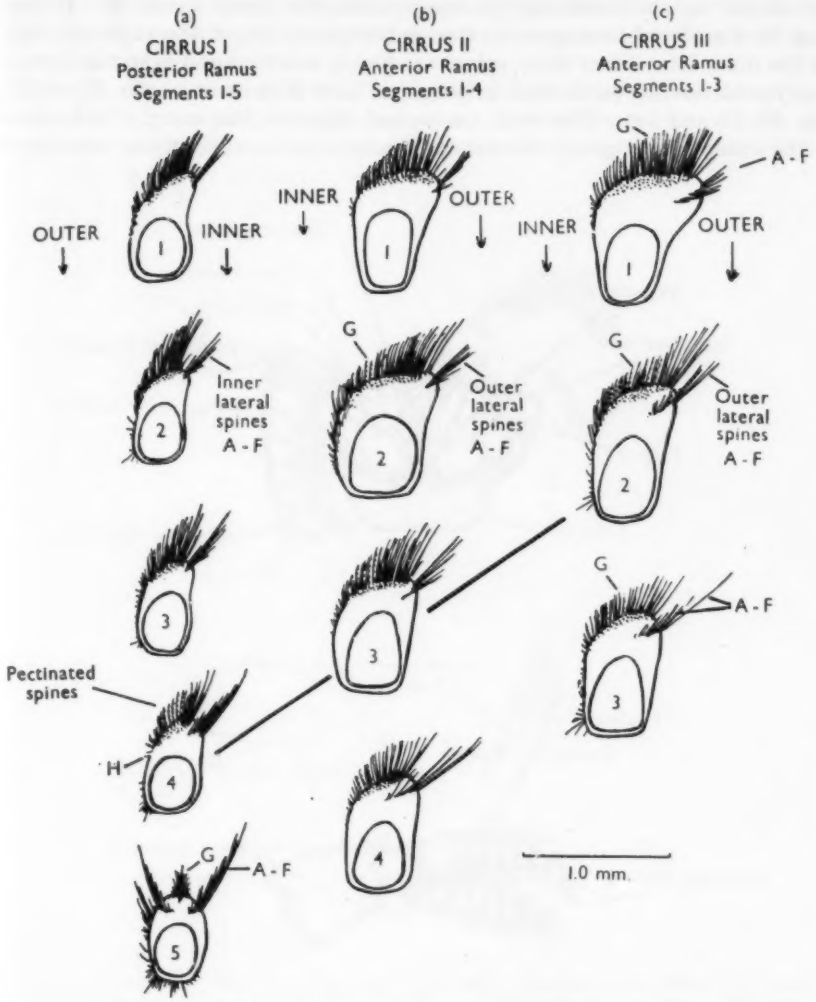

Fig. 3.—Proximal segments of rami of Cirri I–III showing arrangement of spines. Proximal views of whole segments taken as indicated from the right cirri—proximal views drawn since spinous pad and lateral spines curve proximally. In all cases the upper portion (of drawings) faces towards centre of body since these are from right side. Segments numbered from proximal towards distal end. Since Cirrus I has posterior ramus modified it has inner lateral stout spines while Cirri II and III have anterior rami modified and have outer lateral stout spines. Pectinated spines concentrated in more distal segments (especially 2, 3 and 4) as one proceeds from Cirrus III to I, and hence come to the same position relative to the body during the downward and forward movement (Fig. 7). Note that segment 5 of Cirrus I though slightly modified is basically similar to the segments of Cirrus VI (Fig. 2). Segments 5 and 4 of Cirri II and III respectively are modified as shown in Fig. 2. Oblique line indicates apposed segments.

are smaller spines decreasing in size towards the inner lateral face ; these may be considered analogous to the central group (G) of the posterior cirri. At the inner lateral face these spines are highly modified and take the form of singly and doubly pectinated bristles (see also Nussbaum, 1890, Plate IV, figs. 16, 17 and 18). The next, i.e. second segment, has many of the spines of the outer lateral group shorter and there is an increase in the number of

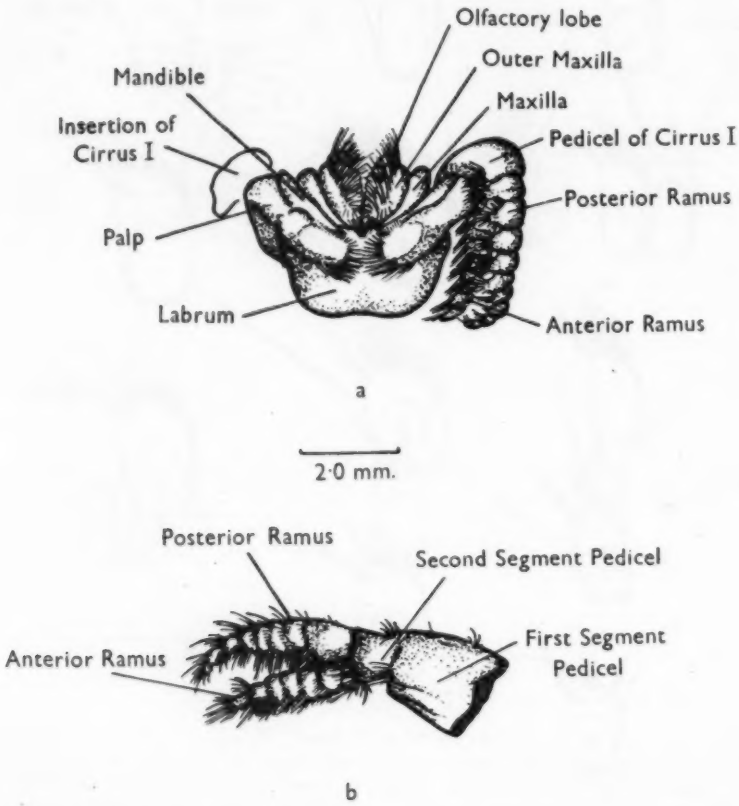

Fig. 4.—Mouth parts and Cirrus I. (a) Mouth parts with Cirrus I drawn to one side. (b) Cirrus I, note contrast in direction of spines on the two rami, those on the anterior ramus pointing distally.

pectinated spines (Fig. 3, Cirrus III, 2). As one proceeds proximally along these three segments the protuberance becomes larger and more asymmetrical.

The general pattern of modification in the four most proximal segments of Cirrus II (Fig. 3, Cirrus II) follows that of the proximal segments of Cirrus III. There is again an increase in asymmetry towards the base and a decrease in length of the outer lateral spines (Fig. 3, Cirrus II, 4 to 1). In contrast to

Cirrus III, however, the pectinated spines are most abundant on the third segment ; the fourth segment, nevertheless, bears many such spines but the first and second only few.

The pedicels of Cirri II and III (Fig. 6) possess aggregations of spines that are formed into groups similar in appearance to those on the pedicels of the posterior rami. However, they tend to be divided into an inner set, which

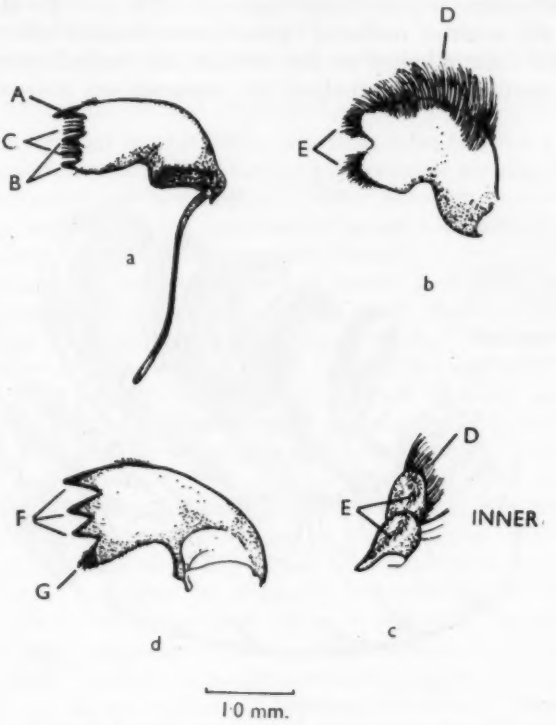

Fig. 5.—Mouth parts. (a) Maxilla—inner view. (b) Outer maxilla—inner view. (c) Outer maxilla—anterior view. (d) Mandible—inner view. (For lettering, see text p. 576, 577).

follows down the line of ' pads ' on the anterior ramus, and an outer set, whose spines point in a posterior direction ; the most distal contain an occasional pectinated spine.

Cirrus I, arising at the side of the mouth (Figs. 4a and 6) is much modified in all segments of both rami (Fig. 4b). In order to facilitate description we may observe that the rami of this cirrus arise from the pedicel at a sharper angle than that taken by those of the other cirri and that in the relaxed position the anterior ramus, pointing almost directly to the anterior, comes to lie, therefore, on the lateral margin of the mouth (Fig. 4a). The four terminal

segments (5 to 8) of the posterior ramus, except for possessing more numerous small spines more widely distributed over its outer distal margin and more profuse and larger ones on the distal-ventral margin, are little different in pattern from those of the posterior cirri (Fig. 3, Cirrus I, 5). The pattern of spines on segments 1 to 4 of this ramus is similar to that of the distal segments of Cirrus II, with an increase proximally in asymmetry and a decrease in the length of the inner lateral spines (Fig. 3, Cirrus I). Pectinated spines are particularly abundant on the fourth segment. The two (or three) terminal segments of the anterior ramus of Cirrus I have a distal collar of outwardly pointing spines slightly longer on the anterior and ventral margins (Fig. 4b). The anterior surface of the proximal five segments are covered with spines

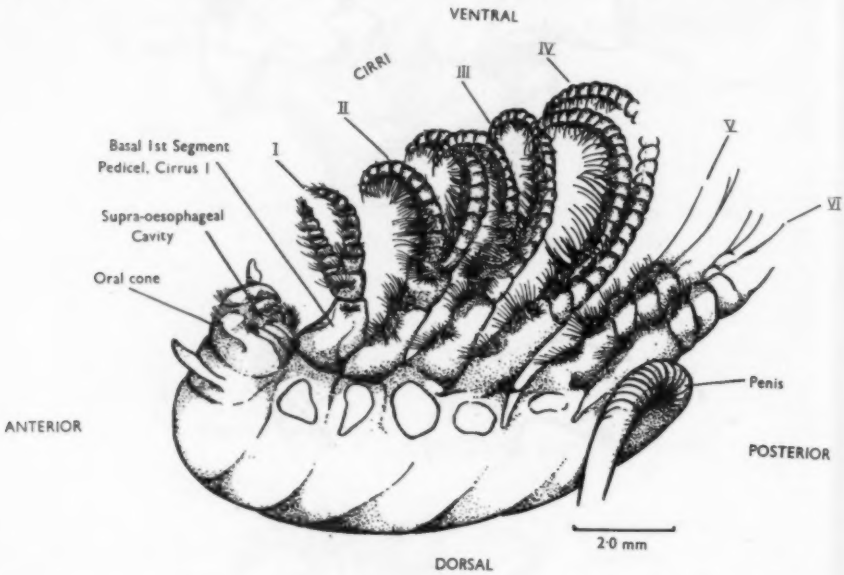

Fig. 6.—Diagram of *P. polymerus* drawn from a cast. Cirri I displaced posteriorly due to flattening. Cirri of one side removed. Filamentary appendages, except oral pair, not shown. Penis turned to one side.

pointing distally and their distal outer margins bear spines directed towards the mouth (Fig. 4a, b). The distal segment of the pedicel has a group of distally pointing spines on its anterior surface and a similar but much smaller group is present on the lower segment (Fig. 6).

The labrum is highly bulbate (Fig. 4a) and its crest bears small teeth and some bristles. The palps, lying across the anterior part of the mouth, are covered with spines, which by their curvature come together on the mid-line and form a basket-like border to the ventral surface of the oral cone (Figs. 4a and 6). The mandibles (Fig. 5d) have three strong teeth (F) whose lower edges are roughened ; the inferior angle (G) bears short, stout, simple spines. Each inner maxilla (Fig. 5a) lies at the inner side of a mandible ; its front

edge is tri-lobed. The uppermost lobe bears two stout spines (Fig. 5a, A) underneath which is a tuft of finer spines ; the central and lower lobes also carry tufts of finer spines (Fig. 5a, B) between which lie rather coarser and longer spines directed somewhat laterally (Fig. 5a, C). The outer maxillae (Fig. 5b, c) each have two blunt lobes, the lower pair curving a little laterally and so away from one another. Each lobe bears on its anterior face a group of simple spines directed towards the labrum ; on the upper lobe the spines are continuous with a further series (largely serrated) that passes over the crest and extends downwards on the inner face (Fig. 5b and c, D). These longer spines are curved both to the anterior and towards the mid-line.

RESPONSES OF THE CIRRI TO TACTILE STIMULATION

Animals maintained in still water will from time to time partly expand and contract the whole cirral net, but such movements are sluggish and infrequent. When transferred to a current of water, however, the animals quickly open and stay expanded ; the experimental work with artificial stimuli has been largely carried out on such expanded animals.

A single ramus, on light touch with a needle, curls towards the mouth, without any response being elicited from the other ramus of the same cirrus or the remaining cirri of the animal (Pl. 2, figs. 7 and 8). That part of the ramus distal to the point of contact reacts (Pl. 2, fig. 9). If a needle is drawn gently down towards the base of the ramus, the latter may be coiled around it (Pl. 2, fig. 8). A stronger tactile stimulus on a single ramus will cause both rami to curl and an even stronger stimulus results in contraction of the whole cirral net and even withdrawal of both cirri and body into the mantle cavity-sometimes followed by closure of the capitulum. This total closure is presumably a defence mechanism against predation or unfavourable conditions. It is possible to elicit the response to light touch by contact with only a few spines. No quantitative observations are available, but after much experience it is believed that the antero-lateral face, well supplied with long spines is much more sensitive than the posterior face with its relative few short spines. It would also appear that there is a directional effect since stimulation is more effective if the spines are bent in a proximal direction. Since it must be presumed that the spines are pressure receptors this may indicate some structural asymmetry in relation to sensory neurons. Repeated stimulation of a ramus results in fatigue. Tactile stimuli may not only cause a cirrus to curl but may also effect bending of the rami towards the mouth.

Stimulation of the pedicels of Cirri IV–VI cause both rami (possibly with a little curling) to bend so that their tips become closely apposed to the mouth parts. In the case of the fourth and fifth cirri this is accompanied by a slight downward and inward movement of the pedicel. On stimulation of the pedicel of Cirri II or III (Pl. 2, figs. 10 and 11) this downward and inward movement is much more marked and gives the appearance of a rotation about the base of the pedicel. If the stimulation is sufficiently strong the proximal 'pad' (see p. 571) of the cirrus may be brought right across the mid-line to touch that of Cirrus II (or I) (Fig. 7a). At the same time the posterior ramus, which under light stimulation may together with the anterior remain extended,

is brought down against the pads of the pedicel and proximal segments of the anterior ramus. It may be noted that stimulation of any part of one cirrus does not inhibit action in any part of the other cirri.

Simultaneous stimulation of the pedicels of Cirri III (or II) cause each to turn inwards and downwards as described above, and to meet on the mid-line (Fig. 7b). This is followed by a similar movement in which each cirrus moves only a short distance while in contact with that of the other side, in general one moving forward as the other moves backwards or remains inactive. This produces what may be termed a ' reciprocating ' action of the cirri, rubbing the basal pads together. On occasions it has been possible to stimulate a

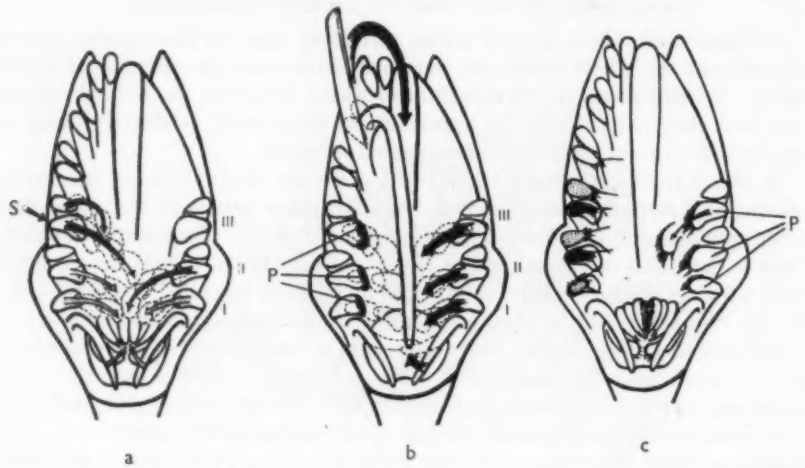

Fig. 7.—Schematic representation of cirral movement. (a) The movement of cirri following stimulation (S) of pedicel. The dark arrows indicate initial movement and the stipuled ones later movement. See also Plate 2, figs. 10 and 11, and text pp. 577-9. (b) Cirrus VI moving anteriorly towards mouth parts with synchronous forward and downward movement of anterior cirri. The basal pads (P) of the latter eventually become juxtaposed on the mid-line to close down on Cirrus VI. See also Plate 1, figs. 2 and 3, Plate 2, figs. 12. and text pp. 577-9. (c) Showing arrangement of basal pads and overlapping consequent on asymmetry as cirri move downwards and inwards. These are eventually juxtaposed—see (a). See also Plate 1, No. 3 and text p. 580.

posterior cirrus, say posterior ramus of Cirrus V (Fig. 7b), and observe a sequence of reactions in which the above simple responses are integrated. The cirrus bends over and as its distal segments come down between the basal pads of the anterior cirri the latter come together in their inward and downward movement clasping the posterior cirrus. As the latter is withdrawn the ' reciprocating ' action of their basal pads follows for a short time.

On stimulation of the small first cirrus the proximal portions of the posterior rami of both sides come together over the mouth and their distal segments, as well as the anterior rami, turn so that they come to lie over and in contact with the edge of the oral cone.

THE BEHAVIOUR PATTERN UNDER NATURAL CONDITIONS

As already stressed the activity of *P. polymerus* is related to water movement ; extension of the cirri and reaction to artificial or natural stimuli depend upon a general level of activity being initiated and then maintained by a flow of water above a certain critical level. In maintaining this level doubtless not only current speed (viscous flow) but also turbulent motion, and the effect of mechanical shock, such as is present in the surf zone, play a part.

Under appropriate conditions the cirri are extended and the body raised in the mantle cavity. Stimulation is then effected by contact with food particles, e.g. planktonic crustacea. Depending upon the intensity of stimulation and subsequent events a whole series of reactions may take place based upon, and integrated from, those described for artificial stimulation and all directed towards capture of prey. For example, if an organism of the appropriate size strikes the distal end of Cirrus VI it may be brought rapidly between the basal pads of the anterior cirri which come together as already described (Fig. 7b, and Pl. 2, fig. 12). If, as a result of struggling, the prey begins to escape more of the cirri may curl to the mouth region and assist in preventing such escape. Should the prey, as a result of struggling, tend to escape as the stimulated cirrus is brought towards the mouth then the other cirri will close down. In this way the cirri come together and their spines overlap so that the cirral nets act as an extremely effective captorial device. Since the cirri require stimulation before reacting, and most frequently react independently, they cover a more effective ' sampling ' area when expanded. Their contraction upon a struggling prey is secondarily elicited and stands in contrast to any filtering function associated with a rhythmical cirral beat.

Once the prey is firmly lodged between the bases of the anterior cirri then rapid and continuous reciprocal movements of these basal portions take place as they rub together. Such ' reciprocating ' movements are also apparent in the posterior rami of Cirri I but with a relatively short to-and fro-movement giving the appearance of reciprocal movement in one plain, namely that parallel to the top of the oral cone. From time to time material is seen to be extruded from between the front of these first cirri (Pl. 1, fig. 6) particularly when much debris is falling on the cirral net. This rejected material must clearly be carried over the mouth parts. Indeed, the impression is gained that when the level of activity is high, and when there is a continuous deposition of light debris falling on and becoming entangled in the cirral net, the latter are being continuously cleaned in this fashion.

THE FUNCTION OF THE SPINES

It has already been noted that the spines of the rami are the seat of the responses to tactile stimulation and that similar responses are obtained by stimulation of some at least of the spines of the basal pads. The orientation of the spines on the distal portions of the cirri serve, as the cirri come forward, to give an effective mechanism preventing the escape of any prey. Not only do the longer distal spines overlap laterally when the cirri come together but, as they curl inwards, the net becomes more effective by the overlapping of the shorter proximal spines of the next more proximal segment (Fig. 2a). The

increased number of spines on the posterior rami of Cirri II and III, their extension further to the posterior on the distal margin and the asymmetry of the stout spines all serve the same purpose, namely to increase the effectiveness of the closing net by engaging across other spines : the modifications in structure and position are required for effective overlap in view of the greater forward and downward movement necessary for the anterior cirri to approach the mouth. The reversal of the asymmetry on the distal segments of the anterior rami of these segments serves the same purpose. The spines on the proximal segments of the anterior rami and on the pedicels of Cirri II and III are, as has been shown, highly modified and, in addition to some of them at least being sensory, their form and arrangement serve an additional mechanical function. The asymmetrical position of the brush like pads on the basal segments of these cirri ensures that after their forward and downward movement the surfaces are closely apposed (Figs. 3, 7b and c) at the appropriate level. In this apposed position the spines point anteriorly and dorsally.

The major spinous pads, namely those possessing modified pectinated spines, since they are set on different segments of the anterior rami of Cirri II and III and the posterior ramus of Cirrus I, are brought to the same level after their movement towards the mouth (Fig. 6). The closure upon the posterior or other cirri, which are subsequently withdrawn, results in prey being ' wiped ' off by these basal pads. The ' reciprocating ' movement that follows results in food being carried forward along and within the basal series of spines, that is, towards the mouth. The orientation of the spines on the basal pads of the cirri is, therefore, such as to form an effective series *after* (and to some extent during) the movement of the cirri towards the mouth. The asymmetry in the position of these spinous pads, as seen in the relaxed outspread state, or when a dissected cirrus is examined has, therefore, functional importance. The form of the spines on the pedicels (Fig. 6), namely, curving strongly to the anterior, ensures that as the cirri move anteriorly prey cannot escape or work its way to the posterior as it is being carried forward by the specialized pads on the anterior rami. The penis, with a series of small projecting spines, normally lying in the mid-line of the body and flanked laterally by the smooth proximal parts of the pedicels, acts as a ' floor ' to the spinous chamber formed by the more distal segments of the cirri (Pl. 1, fig. 1).

The functional significance of the highly modified pectinated spines is not certain. They are so constructed and directed that their pectinated margins could actually engage on a simple spine bearing food material ; as the latter is withdrawn the food particle is then more likely to be retained than would be the case if both spines were simple. They act in fact exactly as their name implies—as combs. They may in addition have a sensory function.

In this way food is brought to the mouth region by the reciprocating movements of the anterior rami of Cirrus I as already described ; in these, the rami of the cirri point almost directly to the anterior (Fig. 4a, b) as they lie together at the sides of the mouth parts. It is difficult to obtain any direct evidence as to how any selection of food is made. Mechanically, if the mouth parts remain inactive and the reciprocating movements of the cirri continue,

any trapped material will of necessity be carried forward over the mouth and rejected. The selection may involve chemo-receptors, which in the presence of unwanted material cause the mouth parts to become inactive although the rejected material may merely consist of all debris of a small size not cleaned off the cirri by the mouth parts as described below.

It has already been noted by Gruvel (1905) and Thomas (1944) that some cirripedes reject material. They further observed that in some species large masses of unicellular glands open on the labrum and at the base of the cirri ; we have seen similar glands in many different species. They were termed 'salivary' glands by Gruvel who suggested that their function was to form a 'bol alimentaire' that was subsequently swallowed. Thomas, however, while also considering that these glands serve to form a ball of material, indicated the process was associated with the rejection rather than the acceptance of material. Such secretions may play a part in the processes described above. Differences in the form of the glands lead Thomas to put forward the suggestion that in sub-littoral pedunculate species rejection of food may not take place, the food rejecting habit being limited to operculates living between tide marks and subject to muddy water conditions. That *P. polymerus* possesses a food rejecting mechanism and is one of the few intertidal pedunculates brings it into line with this suggestion ; for complete confirmation Thomas' hypothesis would require, however, that sub-littoral operculates conform to the general pedunculate pattern. The same author also rejected Gruvel's suggestion that these glands played any part in the formation of a 'bol alimentaire'. We have seen, however, in many histological sections of animals that had been actively feeding, evidence that the food passing down into the oesophagus is stuck together. It seems possible that the secretion of the glands may play a part both in the rejection of food and in facilitating its transfer into, and possibly along, the oesophagus.

THE TRANSFERENCE OF FOOD INTO THE OESOPHAGUS

It is not possible to see the movements of the trophi (Fig. 5) in an intact animal since they are covered by the cirri. The following conclusions are, therefore, based in part on a large number of animals opened up rapidly with the least possible injury and observed under a binocular microscope whilst maintained under water ; under these conditions the mouth parts continue to move and may be stimulated. In addition, animals were observed that had been partially dissected while still attached to the substratum, and then kept in a vigorous current of sea water so that they remained reasonably active for several days. Additional observations have been made on *Balanus nubilus* Darwin ; this animal reaches a large size—10 cm. in basal diameter—and the whole body may be removed with less apparent injury than is the case with *Pollicipes polymerus*. The mouth parts of the former species are large, easy to see and will continue active movements for some time after dissection.

The mouth parts are capable of many and varied movements ; their musculature is complex. It would appear that normally, food brought forward as already described is carried further forward to the region of the mouth by

the outer maxillae moving, rather like a pair of hammers, in the median plane (Fig. 8). Their forward and downward movement in this plane allows their anteriorly directed spines (Fig. 5) to carry the food from the cirri towards the mouth. In general the two outer maxillae seem to move together in *P. polymerus* : they may move separately and tilt apart. In *Balanus nubilus* vigorous reciprocal hammer-like movements of these appendages have been seen. As Darwin (1851) pointed out, food is partly prevented from passing over the labrum by the basket-like network of spines on the immobile palps (Figs. 4 and 8) ; incurling movements of the tips of the anterior and, to some extent, the posterior rami of Cirri I (Fig. 7a) also serve the same purpose. As the outer maxillae bring food down, the inner maxillae and mandibles, again often working reciprocally with each other, move downwards and

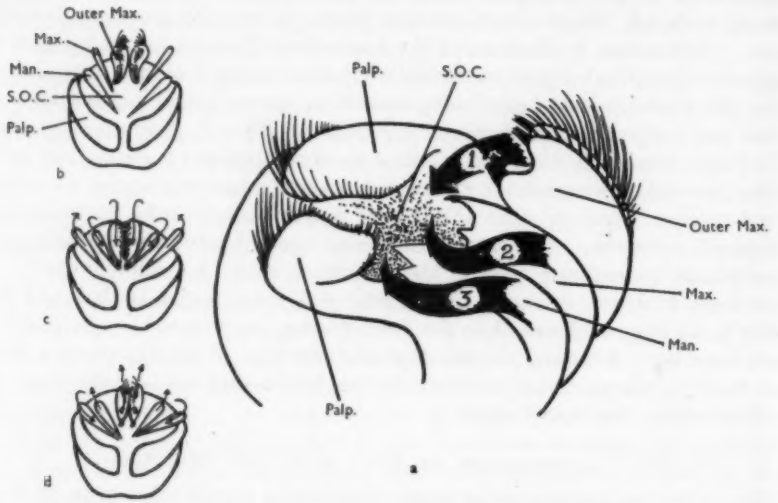

Fig. 8.—Schematic representation of mouth parts and their movements.

(a) Outer maxilla (Outer Max.) moving on mid-line and inner maxilla (Max.) and mandible (Man.) moving downwards and inwards in a curve following the wall of the cavity. Usual order of movement numbered. (b), (c) and (d) Anterio-dorsal view.

inwards along the lateral margins of the labrum in what may be described as a ' digging ' movement (Fig. 8). The spines on the inner maxillae almost meet and become apposed to those carrying food on the anterior faces of the outer maxillae so that, as the latter move backwards, they scrape it off. The mandibles presumably help to carry the food nearer the mouth. There appears to be little mastication, although rapid movement of the mandibles would doubtless tend to tear up larger particles that had reached this region. In addition to the movements by which they carry food into the supra-oesophageal cavity (that region lying over the entrance to the oesophagus), and in addition to some lateral movements both together or independently, the mandibles and inner maxillae show vigorous ' reversal ' movements after they reach the end of the forward and downward stroke. This ' reversal ' consists of an upward

and backward movement—the whole sequence giving the impression that each appendage is moving as on a cam-shaft. The movement appears to be concerned with the rejection of material since, the tips of the appendages remaining together in the first up-stroke, large unwanted masses of material may be thrown upwards from the lower parts of the supra-oesophageal cavity. Such rejection would seem to be additional to, rather than part of, that already described. It has been observed repeatedly in dissected animals and has also been induced by pushing foreign matter into the supra-oesophageal cavity. Further, it often appears to be associated with movements of the oesophageal muscles and although this may be due to the experimental conditions, it seems possible that material which has reached even the oesophagus may, if unpalatable, be regurgitated ; it is then thrown out as described and carried forward by the first cirri.

The movements of the mouth parts of *Pollicipes polymerus* under the various experimental conditions, have been only moderately rapid ; this may reflect the generally sluggish behaviour of the animal or the effect of injury and the unnatural conditions. In *Balanus nubilus* extremely rapid movements have been observed even in animals dissected from the mantle cavity.

Any further movement of the food has not been followed ; Darwin (1851) drew attention to the fact that the oesophagus in the Lepadidae is surrounded by numerous long muscular fascia radiating in all directions and opposing the constrictor muscles and he states that constriction after constriction can be seen to run down its whole course ; in this way food is taken into the oesophagus by a series of violent swallowing movements. *Pollicipes polymerus* appears to be no exception.

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SUMMARY

1. *Pollicipes polymerus*, J. B. Sowerby, a common barnacle in the lower and mid-tide region of the rocky coasts of the Northern Pacific is in part unlike most other common cirripedes in its mode of feeding : it lacks rhythmical cirral activity.

2. The structure of the cirri and mouth parts are described with particular reference to their functional morphology.

3. The arrangement of the spines on the distal segments of the cirri is such that an effective mechanism is ensured to prevent escape of prey as it is transferred to the mouth.

4. The spines on the proximal segments are arranged in groups ; they are so orientated on the anterior cirri that food is scraped off the distal portions of the cirri and subsequently conveyed towards the mouth.

5. The responses of the cirri to tactile stimulation are described : light touch elicits response of a single ramus and with increasing strength of stimulus more of the cirrus and even other cirri may respond. Strong stimulus results in complete closure. The large spines appear to be pressure receptive.

6. Stimulation of the pedicels of the anterior cirri elicit a forward and downward movement towards the mid-line and mouth. This may be followed by what are termed reciprocating movements—each pedical moving to and fro alternately.

7. The integrated pattern of activity following capture is described. In the simplest case prey is brought by a cirrus to the mouth parts where it is ' clasped ' between the pads of the pedicels of the anterior cirri ; on withdrawal food is cleaned off by the latter. If the prey attempts to escape, other cirri react to form a closed basket and their basal portions help to ensure capture.

In some species micro-feeding is important and involves the passage of a current of water over the mouth parts as a result of movements of the body within the mantle cavity even without a full cirral beat (Southward & Crisp, 1958). It is not implied that micro-feeding may not take place in *P. polymerus* as a result of similar activity (Barnes 1959).

8. A food rejection mechanism is described. If the reciprocating action of the anterior cirri continues whilst the mouth parts remain inactive food is carried over the oral cone to be rejected at the anterior. It is not certain whether rejection involves selection by chemo-reception or whether it is purely mechanical depending only on particle size and food consistency.

9. The transference of food to the oesophagus is described. Particles are carried from the bristles of the pedicels of the anterior cirri by the hammer-like movements of the outer maxillae. They are taken from these by the inward and downward movements of the inner maxillae and mandibles and thrust towards the oesophagus. A reversal movement of the inner maxillae and mandibles allows food to be vigorously ejected from the oral cavity.

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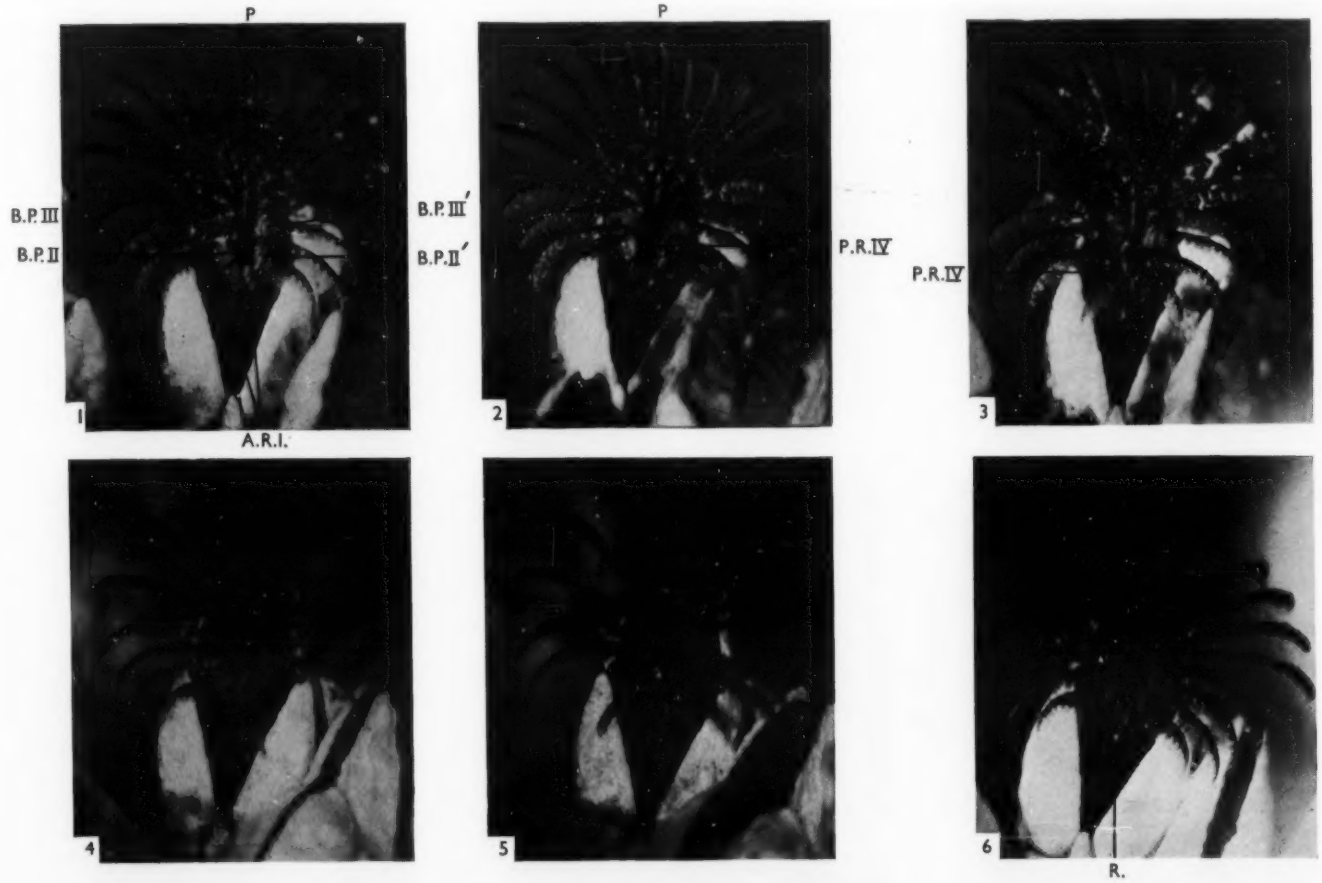
EXPLANATION OF PLATES

Plate 1

Fig. 1.—Cirral net wide open. Penis (P) on mid-line. Basal pads of left Cirri II and III (B.P. II and B.P. III) starting forward and downward movement ; basal pads of right Cirri II and III (B.P. II' and B.P. III') standing somewhat apart from the others and in reciprocating movement. Anterior rami (A.R. I) of Cirri I pointing forward.



Feeding in the pedunculate cirripede, *Pollicipes polymerus*.

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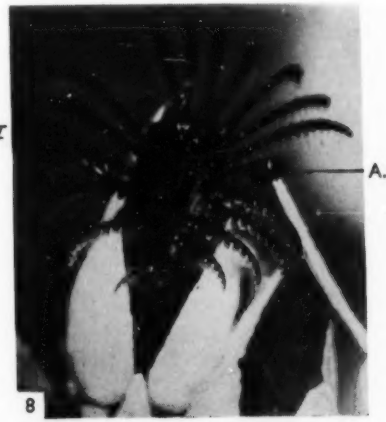

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Feeding in the pedunculate cirripede, *Pollicipes polymerus*.

Fig. 2.—Posterior ramus of Cirrus IV (P.R. IV) curled with its tip to the anterior and about to be ' cleaned ' by the pads of the anterior cirri. Note that the forward and downward movement of Cirri I, II and III has only just begun.

Fig. 3.—Posterior ramus of Cirrus IV (P.R. IV) in between the pads of the anterior cirri which have closed in upon it after completion of their forward and downward movement.

Fig. 4.—Anterior cirri in reciprocating movement after withdrawal of ramus from position indicated in fig. 3.

Fig. 5.—Several rami brought into close apposition with the basal pads of the anterior cirri. This frequently follows the capture of prey by a single cirrus or ramus in order to prevent escape. It may also follow a single large stimulus or multiple stimuli.

Fig. 6.—Anterior rami of Cirri I (A.R.I.) rejecting material (R).

PLATE 2

Fig. 7.—Anterior ramus of Cirrus IV (A.R.IV) curled following tactile stimulation (T.S.).

Fig. 8.—Anterior ramus of right Cirrus IV (A.R.IV) curling about a needle as the latter is drawn from the distal to the proximal part of the ramus. Simultaneously both rami of the left Cirrus V (A.R. and P.R. V) have come forward to the anterior. No inhibition of left side during stimulation of right.

Fig. 9.—Proximal stimulation of the anterior ramus of Cirrus IV (A.R. IV) causing part of ramus distal to the point of contact to curl without any effect on the posterior ramus.

Fig. 10.—Pedicel of Cirrus III (A.R. and P.R. III) about to be stimulated.

Fig. 11.—Forward and downward movement of Cirrus III (A.R. and P.R. III) without curling of the rami followed by stimulation of the pedicel (compare fig. 10).

Fig. 12.—Both rami of Cirrus VI with the tips between the basal pads of the anterior cirri following their synchronous forward and downward movement which has resulted in their separation from the posterior cirri.

ON THE ANATOMY OF TWO SAURICHTHYID FISHES, *SAURICHTHYS STRIOLATUS* (BRONN) AND *S. CURIONI* (BELLOTTI)

BY

JOHN GRIFFITH

*Department of Biology, Guy's Hospital Medical School, London, S.E.*1

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(With 2 plates and 7 figures in the text)

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INTRODUCTION

This paper is based on an examination of the specimens of *Saurichthys striolatus* and *S. curioni* in the British Museum (Natural History), [B.M.(N.H.)]. The specimens of *S. striolatus* have been previously briefly described by Woodward (1895), but a re-examination has shown features which he did not mention and which are of importance when comparing his descriptions with those of other authors. The specimens of *S. curioni* have not previously been described.

Before proceeding to describe the specimens it is necessary to explain the nomenclature used for the dermal bones in this paper.

NOMENCLATURE OF DERMAL BONES

If the skulls of saurichthyids are compared with those of less specialized sub-holostean fishes it becomes obvious that the dermal bones are reduced in number. There are two possible ways in which this condition may have been achieved : (1) by the fusion of primitively distinct elements ; (2) by the loss of certain elements and the expansion of others to fill their places.

In his detailed account of the saurichthyids from Spitzbergen Stensiö (1925) assumes that reduction in the number of dermal bones has occurred by the fusion during ontogeny and phylogeny of originally distinct elements resulting in the formation of complex structures, and by the use of compound names, e.g. supratemporo-intertemporo-extrascapular, nasalo-antorbital,

dentalo-splenial, he indicates the manner in which he believes these fusions to have taken place. Piveteau (1946) and Lehman (1952) employ a similar though not identical system of compound names in their descriptions of the skull of *Saurichthys madagascariensis*. Hauff (1938) in his account of *Acidorhynchus brevirostris* uses simpler names than those used by the authors mentioned above though he too believes that quite extensive bone fusions have occurred.

An objection to this interpretation of the saurichthyid skull is that in none of the supposed compound structures is there any direct evidence of bone fusion such as the presence of multiple centres of radiation of either the ornament or of the bone structure. In this connection Parrington (1956) claims that " since the outstanding variations in the dermal bone patterns of early vertebrates can be accounted for quite closely by simple assumptions concerning the manner of growth and relative positions of their rudiments, assumptions of bone fusion without direct evidence are unjustified ".

In this account I have in the main, used the terminology employed by Hauff (1938) without, however, subscribing to his or Stensiö's views on bone fusion as I believe that, at present, the evidence available is insufficient to enable one to decide confidently the manner in which the number of dermal bones has been reduced.

SAURICHTHYS STRIOLATUS (Bronn)

Synonymy.

1858 *Belonorhynchus striolatus* H. G. Bronn, *Neues Jb. Min. Geol. Palaönt.* pp. 7–12, pl. 1 figs. 1–10, pl. 2 fig. 1.
1866 *Belonorhynchus striolatus*, R. Kner, *S. B. Akad. Wiss. Wien* (1) **53**, pp. 189–197, pl. 6.
1890 *Belonorhynchus striolatus*, A. S. Woodward, *Mem. geol. Surv. N.S.W.* (*Palaeontology*) **4**, pp. 22, 23.
1892 *Saurichthys striolatus*, O. M. Reis, *Geogn. Jh.* **4**, pp. 143–150, fig. 5.
1895 *Belonorhynchus striolatus*, A. S. Woodward, *Cat. foss. fish.* pt. 3, pp. 11, 12.
1925 *Saurichthys striolatus*, E. A. Stensiö, *K. svenska VetenskAkad. Handl.* (3) **2**, No. 1, p. 5.

This species has been described by three authors, namely Bronn (1858), Kner (1866), and Woodward (1895). Comparison of these accounts reveals several discrepancies. For instance, according to Bronn and to Woodward the fin-rays are articulated or jointed, while Kner describes them as unjointed ; the two earlier authors differ in their estimates of the number of rays in the various fins (see Table 1) while Woodward gives no information on this point.

TABLE 1

The numbers of fin-rays in the fins of *Saurichthys striolatus*, as estimated by Bronn (1858), by Kner (1866), and from specimens in the B.M.(N.H.).

Fin	Bronn	Kner	B.M.(N.H.) material
Pectoral	c 25	15–16	c 35
Pelvic	c 12	6–7	18+
Dorsal	18–20	25–26	25+
Anal	18–20	22–24	26–29
Caudal (epichordal lobe)	c 20	13–14	28+
(hypochordal lobe)	c 20	13–14	34–35

Further Bronn describes and illustrates the teeth as short, blunt, peg-like structures, but Kner writes of sharply-pointed, canine-like teeth. All the known material of this species has been collected from Raibl in Austria and no other saurichthyid has been recorded from this locality. In view of this, and of the general agreement by the three authors as to the size and proportions of the fish, the shape of the opercular bone, and the nature of the squamation, it is reasonable to suppose that all the specimens belong to one species. Re-examination with modern techniques of the B.M.(N.H.) specimens with particular reference to the points just enumerated allows of a more detailed description of this species than has hitherto been given. It is also possible to resolve some of the apparent contradictions in the accounts.

Material

The material in the B.M.(N.H.), which also formed the basis of Woodward's account of this species, represents four individuals and an isolated tail. The specimen numbers are : P.966; P.966a, P.3789, P.3789a (counterpart of P.966a), and 33061. The preservation is good with the exception of the head region, the posterior part of which is badly crushed in all four individuals. The specimens were obtained from the bituminous shales of Raibl near Villach in Carinthia, Austria. According to Sherlock (1947) the Raibl beds belong to the Carnian series and are of Upper Triassic age.

Measurements and Proportions

This was a small, elongate, graceful fish (Pl. 1, figs. 1 & 2). The total lengths of over fifty specimens examined by Kner (1866) range from 100 mm. to 181 mm. The measurements of the B.M.(N.H.) specimens are given below (Table 2). The body was remarkably slender ; in the specimens which I examined the maximum depth of the trunk is in the region of 5 mm., and this tapers to only 1 mm. in the caudal peduncle. The skull is unusually long, even for a saurichthyid, it occupies from 40 per cent to 45 per cent of the total length of the animal. The pectoral fins lie close behind the operculum.

TABLE 2

Saurichthys striolatus, measurements.

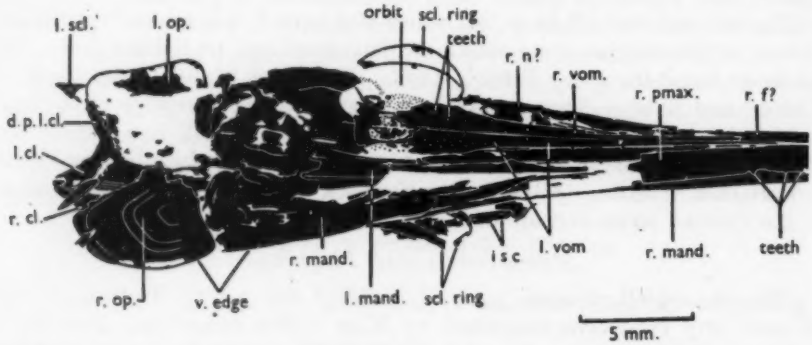
Specimen No.	Total length (mm.)	Length of head including operculum (mm.)
P. 966	128	57
P.3789	153	67
33061	—	59

The very small pelvic fins are borne slightly posterior to the midpoint between the pectorals and the notch of the caudal fin. The dorsal and anal fins lie opposite each other and are placed far back, about halfway between the pelvic and caudal fins. Posterior to these fins the body tapers to the narrow caudal peduncle which bears the large, bilobed caudal fin.

The Skull

The skull is displayed in a similar manner in all the specimens with the exception of P.3789a, the counterpart of P.966a. The neuro-cranium is

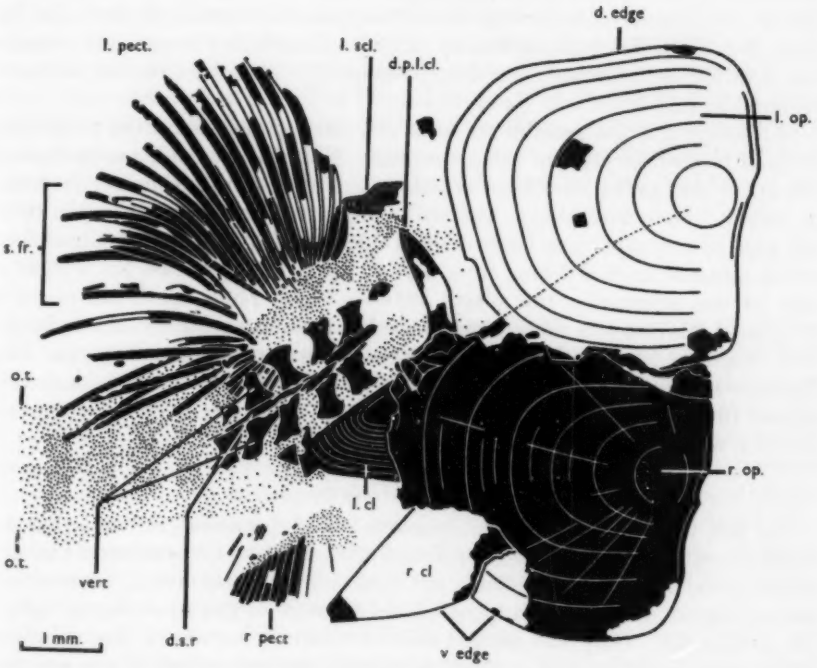
crushed dorso-ventrally, the palatal surface being exposed, while the jaws tend to lie on their sides (Fig. 1). As a result it is impossible to make out much of the skull roof and cheek region. As in all saurichthyids, the skull is prolonged into a finely tapering beak in the formation of which upper and lower jaws take an equal part. This elongation affects the whole head, but its effect is particularly noticeable in the region anterior to the orbit. The length of the head including the operculum is about thirteen times its maximum height. The orbit is oval in shape, approximately 5 mm. long and separated by about its own length from the anterior margin of the opercular bone. In life each eye was protected by a delicate sclerotic ring. This shows no sign of sutures and appears to consist of a single ossification.



Text-fig. 1.—*Saurichthys striolatus*. Posterior part of skull of specimen No. P.3789. Bone solid black, indistinct skeletal material stippled, impressions in outline. (Key to lettering on p. 606.)

The maxilla is expanded posteriorly into a sheet of bone the exact shape of which could not be ascertained. Anterior to the orbit the edge of the upper jaw of each side is formed by a well developed premaxilla. The premaxillae form the sides and much of the dorsal surface of the rostrum, and in addition near its ventral edge each bears a medial lamella which contributes to the formation of the palate. In none of the specimens was it possible to observe the junction, beneath the orbit, of the maxilla and premaxilla but the upper jaw must have been considerably reduced in height in this region. The anterior third of the premaxilla is smooth except for a few fine longitudinal striae ; the remainder of the bone, as far as the orbit, bears striations running at right angles to the edge of the jaw. Where the lower margin of the bone is partly covered with matrix these vertical striations often give the appearance of short, blunt, peg-like teeth ; the " teeth " illustrated by Bronn are probably due to this effect. In two specimens, Nos. P.3789 and 33061, on one side ventral to and slightly anterior to the sclerotic ring are a few delicate pieces of bone some of which have openings suggestive of a sensory canal (Fig. 1, i.s.c.). If this is so the sensory canal must be the infra-orbital and the bones parts of the infra-orbital series.

A little of the palate is shown by all the specimens (Fig. 1). The vomers are slender bones, widest opposite to the anterior portion of the orbit ; in P.3789 each vomer is a fraction more than 1 mm. wide at this point and is at least 16 mm. long. Anteriorly they taper gradually, becoming very narrow. At what appears to be its anterior extremity in P.3789 each vomer is less than 0·2 mm. in width, but there is a possibility that in life even this point was not the extreme anterior end. Posteriorly the vomers narrow more abruptly and, though damaged in all the specimens, they are seen to extend at least to the level of the centre of the orbit. The posterior portion of each bears a number of tooth bases (the teeth themselves are missing) arranged in two, roughly parallel rows. The vomers are bounded laterally by the medial lamellae of the premaxillae which probably met anterior to them. There is no sign of the parasphenoid.



Text-fig. 2.—*Saurichthys striolatus*. Pectoral region of specimen No. P.966a. Bone solid black, indistinct skeletal material stippled, impressions in outline. (Key to lettering on p. 606.)

Nothing is known of the primordial neurocranium and it seems probable that in life this was composed to a large extent of cartilage.

The mandible is powerfully built, the posterior portions of the two rami are very deep and widely separated. Anteriorly they taper, and a short distance in front of the orbit their ventral margins approach each other and join in a long symphysis to form the ventral portion of the beak. Separate

elements could not be distinguished. Below the part of the upper jaw which bears vertical striations the lower jaw is ornamented in a similar manner; the remaining surface is more or less smooth.

The opercular bones appear to have been slightly distorted in some of the specimens (Fig. 1) but in others (Fig. 2) they appear relatively undistorted. In these specimens the opercular is seen to be a relatively large bone, about as long as it is high, with nearly straight anterior and dorsal edges but with rounded posterior and ventral edges. The external surface shows a number of well marked concentric growth lines, and fine radiating striae. No indication of separate subopercular or interopercular bones, or of branchiostegal rays could be observed. As the region where these elements might be expected to occur is the best preserved of the whole skull, it may be assumed that they were not present in life. Stensiö is of the opinion that the large size of the opercular in the Spitzbergen saurichthyids together with the absence in these species of separate subopercular and interopercular bones indicates that the opercular probably incorporates an originally distinct subopercular element and possibly an interopercular element as well. There is, however, no direct evidence in support of this view.

Although it is not possible to make out the complete dentition portions of it could be seen in most of the specimens. Near their extreme anterior ends the upper and lower jaws bear slender conical teeth approximately 0·13 mm. in height. More posteriorly, but still a little distance anterior to the orbit, the edge of the upper jaw bears a small number of widely spaced, blunt teeth which measure up to 0·2 mm. from base to apex. In specimen No. P.3789 on part of the premaxilla the spaces between these blunt teeth are occupied by a large number of smaller, slender teeth a little less than 0·1 mm. in height. The vomerine teeth had slightly oval bases measuring about 0·13 mm. long. The widely spaced, blunt teeth, and the smaller teeth between them did not appear to possess apical caps, but it was not possible to determine whether or not this was also true of the other teeth.

Vertebral Column

In life the vertebral column consisted of a persistent notochord and a series of ossified neural arches lying dorsal to it. Skeletal elements were probably present ventral to the notochord, but these remained unossified except in the caudal region, where they supported the fin-rays of the hypochordal lobe of the caudal fin. Only the ossified structures are preserved in the specimens. Each neural arch consists of a pair of curved elements which lie one on either side of the midline (Fig. 6a). The anterior and posterior margins of each element are concave so that an oval foramen is formed between contiguous elements. These foramina must have served for the emergence of the spinal nerves. The ventral part of each element is thin and slightly expanded, and has a convex ventral margin. In life this portion of the element was probably in contact with the lateral or dorso-lateral surface of the notochord. Dorsally a similar, but more robust, expansion occurs and here each element was in contact with its fellow of the opposite side and also with the contiguous elements on the same side of the notochord. The left and right members of

each pair of elements appear to have been connected to one another along the whole of their dorsal margins though they are not always accurately opposed to each other (Fig. 2, vert.). The exact nature of the connection between the successive pairs of elements could not be observed, but it seems unlikely that this connection was a rigid one as this would have tended to prevent lateral flexing of the vertebral column. Contiguous elements are not in contact ventrally. In the anterior part of the trunk the neural arches are approximately 0·65 mm. high. Posterior to the dorsal and anal fins their size gradually decreases and a little in front of the caudal fin they measure 0·4 mm. in height. The rays of the caudal fin were supported by prolongations of the neural arches, and of the haemal arches which are ossified in this region (Fig. 5). The exact arrangement is not known. The pairs of elements comprising the neural arches may be exposed either from a lateral aspect with the left and right elements partly superimposed on each other (Pl. 1, fig. 3) or alternatively with their dorsal margins in contact and the ventral edges widely separated (Fig. 2). Frequently they are accompanied by scales of either the dorsal or the ventral series; this may give the impression of a continuous series of neural or of haemal spines (Fig. 2) but in regions where the scale rows and vertebrae are distinct there is no evidence of neural or of haemal spines (Pl. 1, fig. 3). The number of vertebrae could not be determined accurately but appears to have been between one hundred and eighty and one hundred and ninety.

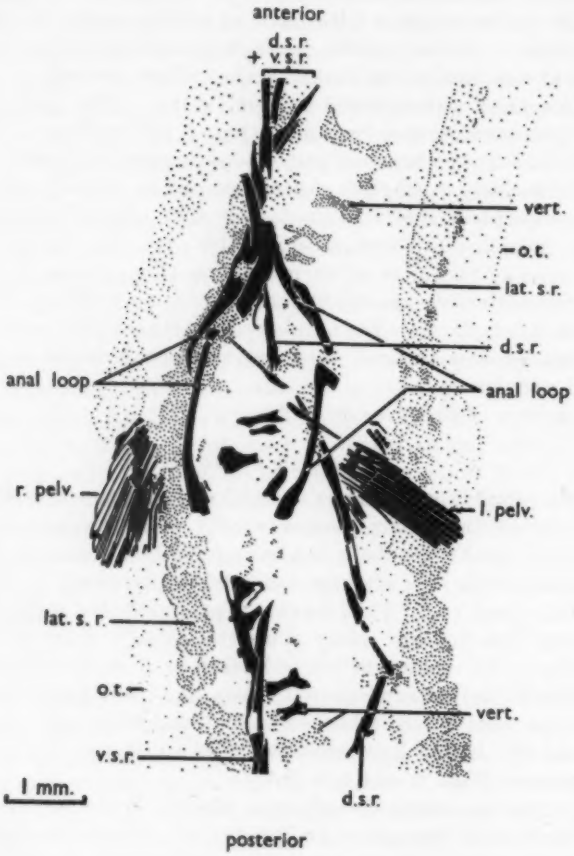
There is no sign of the presence of ribs.

Appendicular Skeleton

Although no single specimen has all the fins intact, it is possible by making a selection from all the specimens to see fairly well preserved examples of all fins except the anal. None of the fins bears fulcral scales and in all of them the fin-rays are unjointed. An attempt was made to ascertain the exact number of rays in individual fins. This, however, proved rather difficult for several reasons: firstly, the fins are rarely complete, usually some of the posterior fin-rays appear to be missing or are so broken as to make counting difficult ; secondly, some of the fin-rays are extremely fine ; and lastly, in some fins a few of the rays seem to have become split into two in the plane of the fin and where the two halves have separated this appears to double the number of fin-rays present (Figs. 2 and 4, s. fr.).

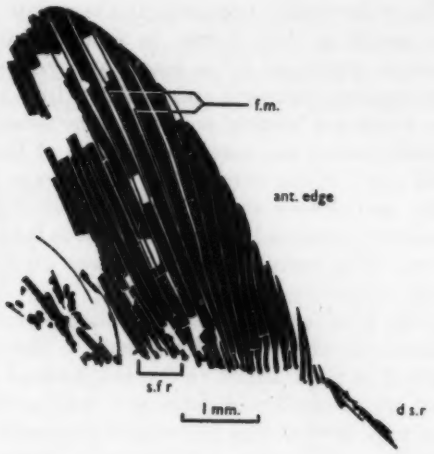
Nothing is known of the endoskeletal portion of the pectoral girdle, and only one of the dermal elements is well preserved. This is the cleithrum (Fig. 2, r. cl., l. cl.) ; it has a small slender vertical portion, the dorsal process, which extends dorsally immediately behind the operculum, and a large horizontal portion the anterior part of which is covered by the ventral margin of the opercular bone so that its full extent is not known. Posteriorly, the ventral portion of the cleithrum tapers and ends in a blunt point. Part of a supracleithral element can be seen in some specimens (Fig. 2, l. scl.). In view of the position, and of the large size, of the cleithrum it seems most unlikely that a clavicle was present. Both cleithrum and supracleithrum bear well marked growth lines.

Each pectoral fin is fan-shaped and of moderate size (Fig. 2). The fin-rays are curved and number about thirty-five in each fin ; none of them branch. The anterior fin-rays increase in length until the fifth ray after which there is little or no change in the length of the rays. In one specimen, No. P.966, faint traces of four or five cartilaginous radials can be seen as darker areas in the carbonaceous film left by the soft tissues.

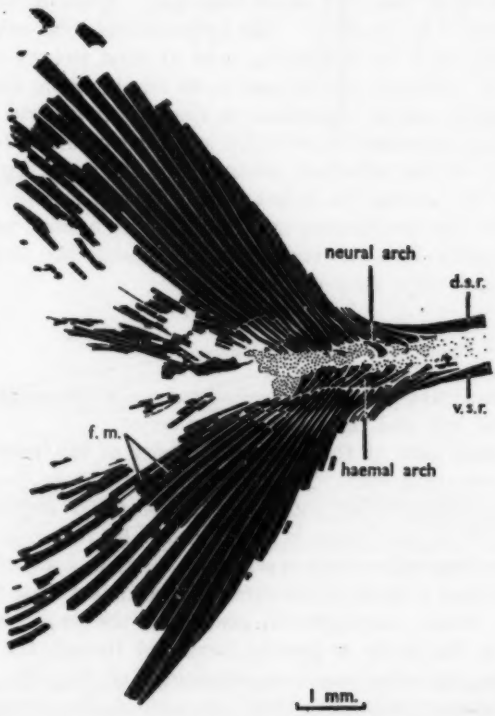


Text-fig. 3.—*Saurichthys striolatus*. Pelvic region in ventral view, specimen No. P.966. Bone solid black, indistinct skeletal material stippled, impressions in outline. (Key to lettering on p. 606.)

There is no indication of the pelvic girdle in any specimen. It is probable that it was cartilaginous. The pelvic fins are very small (Fig. 3). Each is approximately 2 mm. long by 1 mm. broad, and is composed of at least eighteen very fine, closely arranged fin-rays which show no sign of branching.



Text-fig. 4.—*Saurichthys striolatus*. Dorsal fin of specimen No. 33061. Bone solid black, impressions in outline. (Key to lettering on p. 606.)



Text-fig. 5.—*Saurichthys striolatus*. Caudal fin of specimen No. 33061. Bone solid black, indistinct skeletal material stippled, impressions in outline. (Key to lettering on p. 606.)

The dorsal fin (Fig. 4) is roughly triangular in shape with a rounded anterior edge. It reaches a height of from 5 mm. to 6 mm., and a length of from 3 mm. to 4 mm., and is supported by at least twenty-five flattened fin-rays. The fin-rays increase regularly in height and thickness from the first backwards, and their free ends, which are acutely pointed in the anterior region, become more and more rounded until the maximum height of the fin is reached at about the fourteenth ray. Posteriorly to this the fin-rays decrease in height, become more slender, and show a slight distal bifurcation.

The anal fin appears to be similar to the dorsal but in the specimens available is less well preserved. The number of fin-rays was at least twenty-six and possibly twenty-eight or twenty-nine.

The caudal fin (Fig. 5) is large, bilobed and almost perfectly symmetrical. It is of the type known as abbreviate diphycercal. The maximum distance across the fin measured at right angles to the longitudinal axis of the body is 11 mm. Both lobes are rounded and there is a well marked notch between them. The anterior rays in each lobe increase in size until the ninth or tenth after which they decrease in length and thickness, slowly at first and then more rapidly, to the fork of the fin where they are short and very slender. Commencing with the longest, the rays on the posterior edge of each lobe are each distally divided into two short branches. There is no sign of jointing even at the point of bifurcation. The hypochordal lobe contains thirty-four or thirty-five rays and the epichordal lobe at least twenty-eight. However, some of the more posterior rays appear to be missing from the epichordal lobe in all the specimens and it is possible, in view of the general symmetry of the caudal fin, that the number of rays in this lobe too was thirty-four or thirty-five. The termination of the vertebral column, and the exact arrangement of the endoskeleton of the caudal fin is not shown by any specimen. Nevertheless it is clear, firstly that the fin-rays are supported by ossified neural and haemal spines, and secondly that the endoskeletal elements are less numerous than the dermal fin-rays that they support.

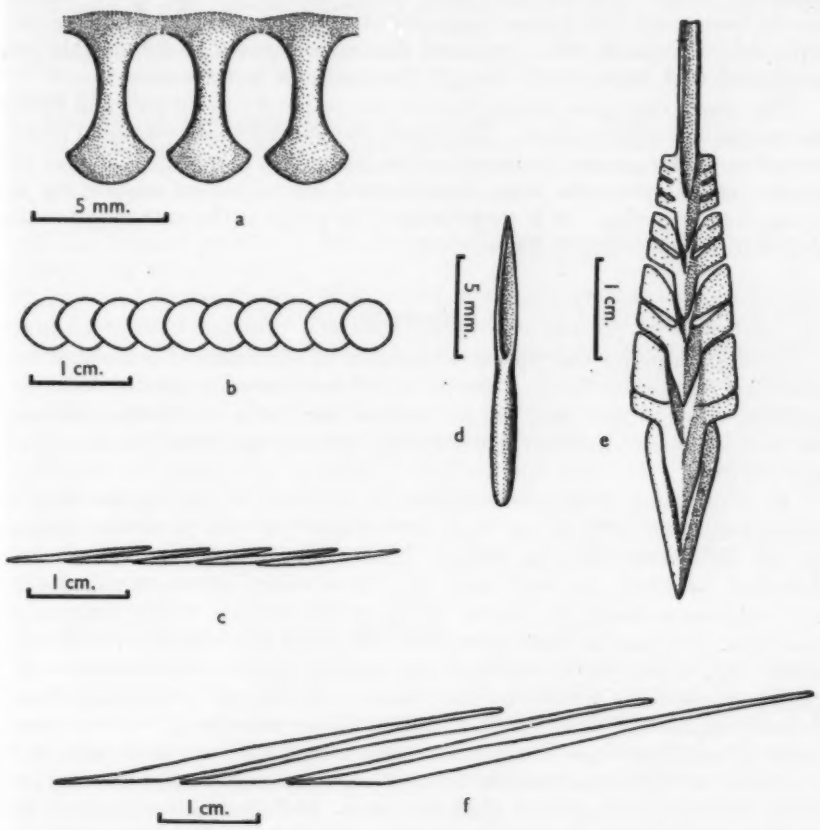
Squamation

The scales are arranged in four longitudinal series ; these are the mid-dorsal, mid-ventral, and left and right lateral line series.

In the anterior part of the trunk the scales of the mid-dorsal series are small, and narrow (Fig. 6d). They are approximately 1·4 mm. in length, pointed at their anterior inner ends and rounded at the exposed posterior end. The anterior part of each scale is grooved for the reception of the posterior part of the preceding scale which overlies it. Farther back the scales increase a little in length and in front of the dorsal fin become a little broader. Behind the median fin, which interrupts the scale row, the length of the part of the scale inserted in the body is greatly increased though the portion exposed remains of much the same length as anteriorly (cf. Fig. 6f). A little farther back, on the caudal peduncle, these elongate scales shorten, broaden and develop wide lateral flanges (Fig. 6e) which reach well down on both sides of the peduncle, and with the similar scales of the ventral series form an almost

complete covering for this region. Immediately in front of the caudal fin the last one or two scales lack the flanges and are almost triangular in shape.

The scales of the mid-ventral series are similar to the corresponding dorsal scales with the exception that in the pelvic region the mid-ventral scale row



Text-fig. 6.—*Saurichthys striolatus*. Reconstructions of : **a**, ossified dorsal elements of vertebra column, lateral view ; **b**, lateral scale row, lateral view ; **c**, ventral scale row in mid-trunk region, lateral view ; **d**, single scale from dorsal scale row, dorsal view ; **e**, dorsal scale row immediately anterior to caudal fin, dorsal view ; **f**, ventral scale row a little distance posterior to anal fin, lateral view. Anterior is to the right in **b**, **c**, and **f**, and towards the top of the page in **d**, and **e**.

divides and reunites in such a manner as to form an oval anal loop approximately 5 mm. long by 1·5 mm. wide (Fig. 3). In life this loop probably encircled the openings of the alimentary and urinogenital systems. The exact arrangement of the modified scales in this region could not be determined

but it seems to conform to a constant pattern ; eight scales appear to be involved. The pelvic fins lie one on each side of the anal loop.

The scales of the lateral line series are approximately circular in shape, very thin and of small size measuring 0·25 mm. to 0·5 mm. in diameter (Fig. 6b). They decrease gradually in size posteriorly but show little, if any, change in shape. In a few of them small circular apertures can be seen, one in each scale. It seems reasonable to suppose that these scales were intimately associated with the lateral line sensory canal, and that this communicated with the exterior through the apertures in the scales.

The lateral scale rows appear to have served chiefly to support and protect the lateral line sensory canal. The dorsal and ventral scale rows seem to have served partly for general protection of the body and, in addition, in the very slender caudal peduncle must have formed an important supporting and strengthening system. It is possible that the scales of the anal loop too may have had a supporting function.

Remarks

In the foregoing description a number of structures have either been described for the first time or else have been considered in greater detail than hitherto. In the first class are the vomers and parts of the squamation, in the second are the dentition, the vertebral column, the dermal pectoral girdle and the fins.

It is necessary briefly to compare my account of this species with the earlier descriptions by Bronn, Kner and Woodward with particular reference to the differences between them. Firstly, the blunt peg-like structures described by Bronn as teeth were, as I have stated above, so-called owing to a misinterpretation by Bronn of the ornamentation of the rostrum and mandible. On part of these structures this takes the form of vertical ridges which can, when partly obscured by matrix, produce an arrangement of peg-like projections similar to the " teeth " illustrated by Bronn. Sharply pointed canine-like teeth as described by Kner were found in the anterior parts of both upper and lower jaws. Secondly, I have no doubt that in the specimens which I examined the fin-rays were unjointed in all fins, even those fin-rays which bifurcate near their free ends. My observations support those of Kner in this respect and disagree with the descriptions of jointed fin-rays in the accounts of Bronn and Woodward. I can only suggest that these two authors must have been misled by artificial breaks in the rays. Thirdly, as can be seen in Table 1, in the case of all fins except the dorsal, my estimate of the number of fin-rays is higher than that of either Bronn or Kner. In the case of the dorsal fin my estimate agrees with that of Kner and is higher than Bronn's. The differences in the various descriptions of this species are probably due to the fact that much of the detail of the structure of this fish is exceedingly fine, for instance the pelvic fin contains rays only 0·05 mm. in diameter, and this detail is difficult to elucidate even with modern techniques and the use of optical equipment which was not available to the earlier workers on this species.

SAURICHTHYS CURIONI (Bellotti)

Synonymy

1857 *Ichthyorhynchus curioni* C. Bellotti in A. Stoppani, *Studii Geol. e Palaeont. Lombardia* pp. 436, 437.
1855–1873 *Ichthyorhynchus Curioni*, O. G. Costa, *Ittiologica fossile Italina* p. 63, pl. 5, figs. 2, 2a.
1863 *Ichthyorhynchus Curionii*, G. Curioni, *Mem. R. Ist. lombardo Sci.* (2) **3**, p. 265.
1886 *Belonorhynchus cfr. robustus* (Bellotti). F. Bassani, *Atti Soc. ital. Sci. nat.* **29**, pp. 33, 34.
1889 *Ichthyorhynchus Curioni*, W. Deecke, *Palaeontographica* **35**, p. 127.
1891 *Belonorhynchus robustus* (Bellotti) [*partim*]. A. de Zigno, *Mem. Accad. Lincei* (4) **7**, p. 53.
1892 *Belonorhynchus macrocephalus* Deecke [*partim*]. F. Bassani, *Mem. Mat. Roma* (3) **9**, no. 3, p. 6.
1895 *Belonorhynchus macrocephalus* [*partim*], A. S. Woodward, *Cat. foss. fish.* pt. 3, p. 13.
1906 *Belonorhynchus cfr. robustus*, O. Abel, *Jb. geol. Reichsanst.* (*Bundesanst.*) *Wien* **56**, p. 7.
1910 *Belonorhynchus Curionii*, G. de Alessandri, *Mem. Soc. ital. Sci. nat.* **7**, pp. 59–61, pl. 4, fig. 3.
1931 *Belonorhynchus curionii*, J. Brough, *Proc. zool. Soc. Lond.* **1931**, p. 293.

All the Triassic species of *Belonorhynchus* were transferred to the genus *Saurichthys* by Stensiö (1919).

The published descriptions of *Saurichthys curioni* contain comparatively little of anatomical interest. The most complete is that by Alessandri (1910). In his account of the skull and pectoral girdle he does little more than describe the ornamentation and mention a few of the more obvious bones, such as the premaxillae, dentaries, "articulo-angulars", opercular, and "claviculars". His account contains one photograph of a specimen crushed laterally, the parts of which are unlabelled, but no other illustration of this species. Examination of a specimen in the B.M.(N.H.) has made it possible to reconstruct the major part of the skull roof and to add considerably to our knowledge of this species, and in the light of this new information to reconsider the relationship of this species to *S. robustus*.

Material

The account which follows is based on two hitherto undescribed specimens in the B.M.(N.H.). One of these, specimen No. P.19300, displays the dorsal surface of the skull together with the dermal pectoral girdle and part of the mid-dorsal scale row. The second specimen, No. P.19312, also a skull, appeared at first sight to be of little value but when radiographed, displayed considerable detail especially of the dentition. Unfortunately, though, this second specimen comes from the type locality of *S. curioni*, the absence of diagnostic characters makes it impossible to refer it with absolute certainty to this species.

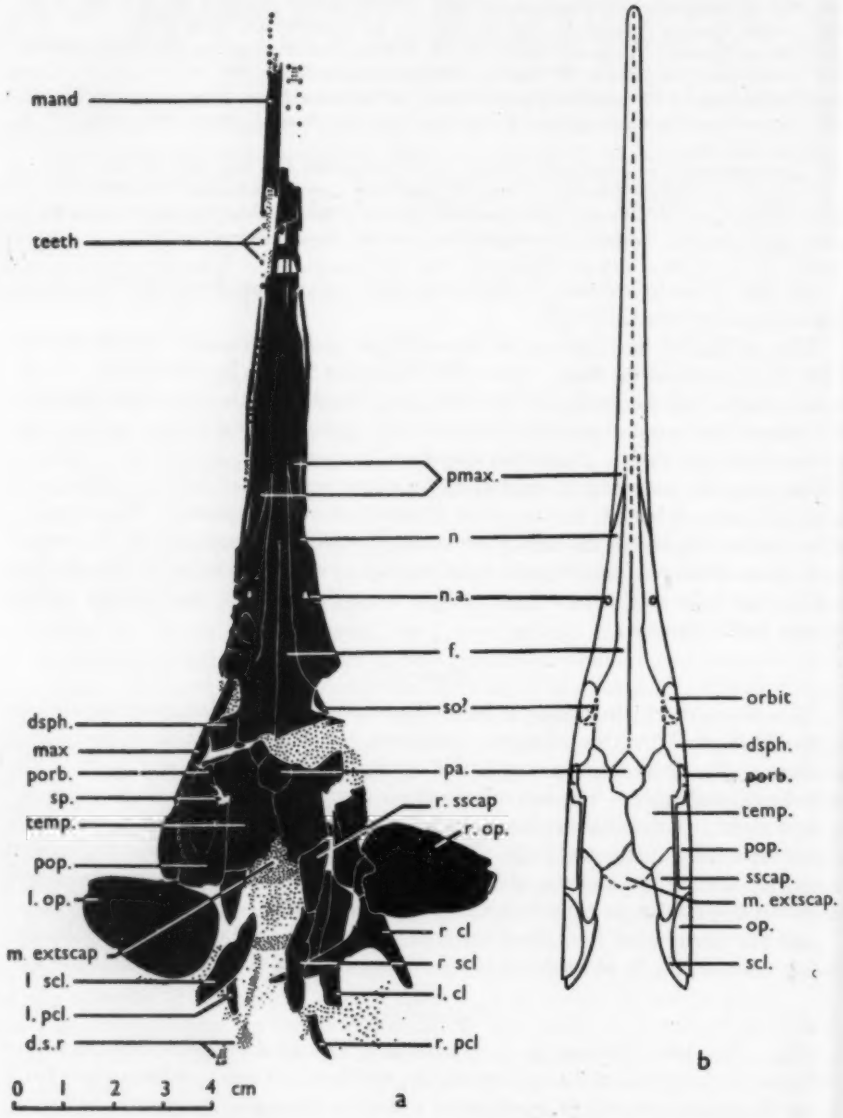
All the material of *S. curioni* has been collected from Bessano in Lombardy, Italy. According to Brough (1939) the Besano fauna is of Middle Triassic age.

Measurements

The complete skeleton is not known. The skull of P.19300 measures 193 mm. in length and has a maximum width of 45 mm. Alessandri (1910) gives the measurements of a specimen which he examined as length 145 mm.; maximum width, 43 mm. The skull of P.19312, doubtfully referred to this species is slightly smaller and has a length of 120 mm. It seems probable that individuals of this species attained a total length of from 50 cm. to 65 cm.

The Skull

The head was long and pointed as in all saurichthyids (Fig. 7). The exact shape of the orbits is not known, but they were relatively not very large, their



Text-fig. 7.—*Saurichthys curioni*. **a**, specimen No. P.19300. Bone solid black, indistinct skeletal material stippled, impressions in outline. **b**, reconstruction of skull in dorsal view based on specimen No. P.19300. (Key to lettering on p. 606.)

length being contained between twenty and twenty-five times in the length of the head. They lie at a distance from the anterior end of the rostrum equal to a little less than three quarters of the total skull length.

In specimen P.13900 the anterior half of the skull is badly crushed and I was unable to distinguish the boundaries of any elements in this region (Fig. 7). The frontals are a pair of elongate bones. They are fairly wide posteriorly but, just anterior to the orbits, they narrow considerably and extend forwards between the narial openings. Their anterior limits could not be observed in the specimen. Each frontal shows a short longitudinal ridge commencing opposite the centre of the orbits and running forwards near to and parallel with the medial border of the bone. It seems probable that this marks the position of part of the supraorbital sensory canal. There is a single, median parietal element (Fig. 7, pa.). This is hexagonal in shape and has one side in contact with each frontal. On either side of the parietal and meeting in the midline behind it lie a pair of large temporal bones of complicated shape. Posterior to these bones in the midline lies a small area of badly preserved bone, the outline of which is indistinct. Judging by its position this may represent the medial-extrascapular elements.

The cheek region of the specimen is badly distorted and although portions of various elements could be observed their boundaries could not be accurately determined. The margin of the upper jaw was formed by the premaxilla and maxilla, and portions of these two bones can be seen in the specimen. Much of the dorsal and posterior margins of the preopercular are preserved, and these abut against the temporal and opercular bones respectively, but the ventral boundary with the maxilla could not be seen. Posterior to the left orbit is a small dermosphenotic element in contact with the frontal and temporal bones. A small portion of the corresponding element can be seen on the right side of the specimen. Also on the right side is a small crescent-shaped bone lying in or near the dorsal margin of the orbit. It is not clear if this is a supraorbital element or merely a detached portion of the right frontal. Anterior to the orbits and in contact with the lateral edges of the frontals are the paired nasal bones which taper anteriorly and end against the premaxillae. The nasals surround the narial openings. Only one such opening could be detected on each side of the skull but the state of preservation of this region is such that it is impossible to be certain whether a second pair of openings were present or not.

Very little of the lower jaw of the specimen is exposed and, apart from the fact that it extends as far forwards as does the rostrum and takes an equal part in the formation of the beak, little is known of its structure in this species.

The opercular bone (Fig. 7a), is a large rounded plate longest near its dorsal edge, in which region the length is equal to approximately three-quarters of the maximum height. The anterior margin, which is almost straight, is notched a little above the mid-point. There is no separate subopercular element.

The frontal, dermosphenotic and nasal bones are ornamented with tubercles of ganoine. On the parietal, temporal, preopercular and maxillary bones these are replaced by ridges, which on the posterior part of the temporal are roughly

parallel and directed posteriorly, but elsewhere tend to anastomose so as to produce a pitted surface. Anterior to the orbit the sides of the rostrum, and possibly also of the lower jaw, appear to have been ornamented with fine, parallel, wavy ridges at right angles to the edge of the jaws. The external surface of the opercular bears well marked, concentric growth lines, and irregular wavy ridges ; the latter are especially prominent in the anterior half of the bone (see Pl. 2, fig. 1).

Two types of teeth are present ; large, sharply pointed, conical teeth arranged singly and at intervals in a longitudinal series near the edge of each jaw ; and more numerous, smaller blunter teeth, which occur between the larger teeth near the edge of the jaw and also, in the anterior part of the mouth at least, nearer the midline. According to Alessandri (1910) the teeth of the upper jaw are, on the whole, more robust than the corresponding teeth of the lower jaw, but I was unable to verify this with the material available to me.

In specimen P.19312 doubtfully referred to this species, radiographs show that although conforming to the description given above, the teeth, of the upper jaw at least, are not regularly and evenly arranged throughout the entire length of the jaw (Pl. 2, fig. 2). For instance, the larger teeth, though borne singly and at wide intervals over much of the jaw's length, are crowded together a little distance in front of the level of the orbit in a position which probably corresponds to the posterior portion of the palatal extension of the premaxilla. Again, the smaller teeth that lie between successive larger teeth in the longitudinal series near the edges of the jaws tend to occur in small groups, usually of three teeth, the centre one of each group being slightly larger than the others.

Vertebral Column

The vertebral column was not visible in any of the material of this species available to me, and it has not been described in previous accounts.

It is not known if ribs were present.

Appendicular Skeleton

In specimen P.19300 the dermal bones of the pectoral girdle are well displayed, though slightly displaced from their normal position (Fig. 7 a). There are at least three, and probably four, dermal elements in each half of the girdle. These are as follows : (1) the suprascapula, a small triangular bone with its base in contact with the posterior edge of the corresponding temporal bone of the skull, and its apex directed posteriorly. (2) Behind the suprascapula, and in life probably partly overlain by it, is a curved supracleithral element which in turn probably overlay the dorsal portion of the cleithrum. (3) The cleithrum, called the clavicular by Alessandri and earlier authors. This is the largest dermal element in the girdle. It consists of a narrow, vertical dorsal process tapering towards its upper end, and a slightly larger, horizontal, ventral portion at right angles to the dorsal process. The whole resembles an inverted T in shape. (4) In addition to the elements already described there is, on each side, a small curved bone lying posterior

to the others (Fig. 7a, l. pcl., r. pcl.). This is probably a postcleithrum. All these dermal elements are ornamented externally with irregular ridges. On the cleithrum the ridges are approximately parallel to the margin of the bone. On the other elements they run more or less parallel with the long axis of the bone. Nothing is known of the pelvic girdle or of the endoskeletal portion of the pectoral girdle.

The fins are poorly preserved in all known specimens ; the structure of the caudal fin alone is known in any detail. According to Alessandri the caudal fin is bilobed and each lobe contains approximately thirty-six fin-rays. These are thick and slightly flattened, and their surfaces are tuberculated.

Squamation

Four longitudinal scale rows were present as in *S. striolatus*. The scales of the mid-dorsal row immediately behind the skull in specimen P.19300 are triangular in shape with the apex directed posteriorly and overlapping the anterior portion of the succeeding scale. A specimen described by Alessandri shows the poorly preserved remains of a dorsal, or anal fin, together with part of the dorsal, or ventral, scale row, the scales of which are similar in shape to those described above. The same specimen shows parts of the lateral scale rows. The scales in these are closely arranged and rhomboidal in shape with the long diagonal parallel to the longitudinal axis of the fish and with the pointed posterior angle overlapping the succeeding scale.

In his original description Bellotti also ascribed to this species some impressions of skin with coarse, rounded granulations which Costa has reproduced in his " Ittiologica fossile Italiana ". Alessandri (1910) is of the opinion that these impressions of skin cannot be identified confidently as belonging to the genus *Belonorhynchus* (=*Saurichthys*). A view with which I agree.

Remarks

As it has been possible to adduce some new facts concerning *S. curioni* it seems worthwhile to draw attention to the doubts that have existed for a considerable time over the separate identity of the species *S. curioni* and *S. robustus* and to reconsider this problem.

The original description of *S. curioni* was published by Bellotti in 1857, who described some fossils from Besano under the name of *Ichthyorhynchus curioni* (=*Saurichthys curioni*). Some years later he entered a brief description of some other, similar remains from Perledo, also in Lombardy, in the manuscript catalogue of the Milan Museum, and to these he gave the specific name of *Belonorhynchus robustus*. The first published description of these specimens from Perledo was given by Bassani in 1886. In his account Bassani used the specific name *Belonorhynchus robustus* (=*Saurichthys robustus*) which he attributed to Bellotti on the basis of the latter's unpublished catalogue. Since then doubt has frequently been expressed as to whether these remains from Besano and Perledo represent one or two distinct species. Most authors, Bassani, Deecke and Alessandri among them, have admitted the possibility that these fossils may be conspecific and have come to the conclusion that

this problem cannot definitely be resolved until we have more information, particularly concerning the postcranial skeleton of the remains from Besano.

The available evidence may be summarized as follows. The skulls are very similar not only in size and shape but also in the nature of the ornamentation, and the scales of the longitudinal scale rows, in so far as they are known in the Besano material, are identical with the corresponding scales in the Perledo specimens. On the other hand there are several points in which the Besano and Perledo specimens differ. Firstly, both Deecke (1889) and Alessandri (1910) agree that the specimens from Perledo have a pair of trapezoidal parietal bones, whereas specimen No. P.19300 which comes from Besano has a single median, hexagonal parietal. Secondly, according to Alessandri (1910) the bilobed caudal fin of *S. curioni* has approximately thirty-six fin-rays in each lobe and these rays are more flattened, and less strongly tuberculated than the corresponding fin-rays of *S. robustus*, which number approximately forty per lobe. These differences however, may easily be due to individual variation or to accidents of preservation. Thirdly, the two localities are thought to be of different geological age. According to Brough (1939) the Besano fauna is of Middle Triassic age and the Perledo fauna is of Lower Upper Triassic age. A comparison of the fish faunas of the two localities as tabulated by Brough (1931) gives the following results :

	Perledo	Besano	In common
Genera recorded	13	10	4
Species recorded	23	13	none

In addition it may be asked why, if one species of *Saurichthys* is common to both localities, do not the two other species of *Saurichthys* from Besano, *S. stoppanii* and *S. intermedius*, also occur at Perledo.

From this summary I think it can be seen that while little of the evidence is conclusive by itself, taken altogether it seems more probable that *S. robustus* and *S. curioni* are two distinct, though obviously similar and probably closely related, species.

SUMMARY

1. An examination of the literature, and of material in the B.M.(N.H.) has shown that earlier accounts of *Saurichthys striolatus* are in part contradictory and inaccurate, and has added to our knowledge of this species.

2. The skeletal system of *S. striolatus* is described.

3. The skull roof of *S. curioni* has been reconstructed from a specimen in the B.M.(N.H.), and a figure of the reconstruction is included. The skull and dermal pectoral girdle are described in greater detail than hitherto.

4. *Saurichthys curioni* and *S. robustus* are compared. The evidence available is considered to indicate that these two species are separate and not conspecific as several authors have believed possible.

ACKNOWLEDGMENTS

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I wish to express my thanks to Professor G. E. H. Foxon in whose department this work was carried out, for help and encouragement, to Dr E. I. White for advice and criticism, and to the Trustees of the British Museum (Natural History) for the loan of specimens.

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EXPLANATION OF THE PLATES

PLATE 1

Fig. 1.—*Saurichthys striolatus*. Specimen No. P.3789.

„ 2. *S. striolatus*. Specimen No. 33061.

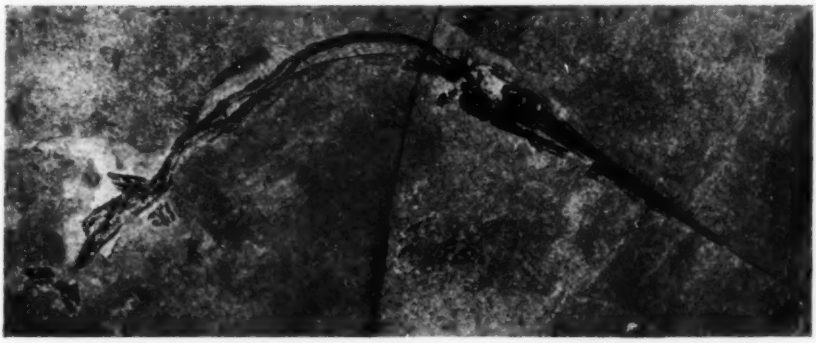
„ 3.—*S. striolatus*. Portion of trunk region of specimen No. P. 3789, approximately midway between the pectoral and pelvic fins. (Key to lettering on p. 606.)

PLATE 2

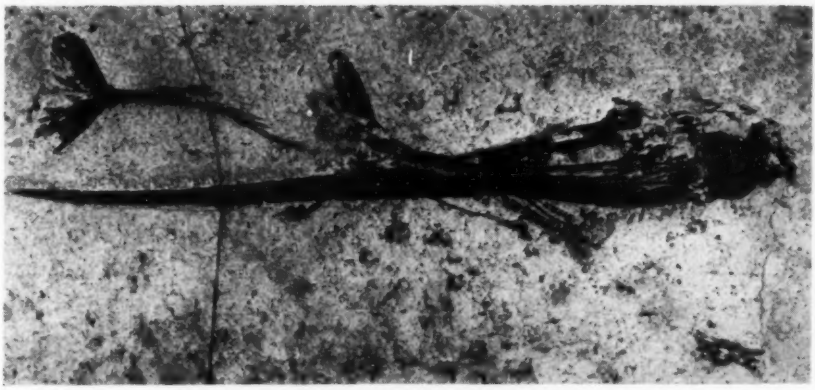
Fig. 1.—*Saurichthys curioni*. Posterior part of specimen No. P.19300.
„ 2.—*S. curioni*. Positive print from radiograph of specimen No. P.19312.

KEY TO THE LETTERING OF THE FIGURES AND PLATES

d. edge.	dorsal edge of bone.
d.p.l.cl.	dorsal process of left cleithrum.
dsph.	dermosphenotic.
d.s.r.	dorsal scale row.
f.	frontal.
f.m.	fin membrane.
i.s.c.	infraorbital sensory canal.
lat. s.r.	lateral scale row.
l.cl.	left cleithrum.
l. mand.	left mandible.
l. op.	left opercular.
l. pol.	left postcleithrum.
l. pect.	left pectoral fin.
l. pelv.	left pelvic fin.
l. scl.	left supracleithrum.
l. vom.	left vomer.
mand.	mandible.
max.	maxilla.
m. extscap.	medial extrascapulae.
n.	nasal.
n.a.	nasal aperture.
op.	opercular.
o.t.	outline of trunk.
pa.	parietal.
pmax.	premaxilla.
pop.	preopercular.
porb.	so-called suborbital.
r. cl.	right cleithrum.
r. f. ?	probably the right frontal.
r. mand.	right mandible.
r. n. ?	probably the right nasal.
r. op.	right opercular.
r. pol.	right postcleithrum.
r. pect.	right pectoral fin.
r. pelv.	right pelvic fin.
r. pmax.	right premaxilla.
r. scl.	right supracleithrum.
r. sscap.	right suprascapula.
r. vom.	right vomer.
scl.	supracleithrum.
scl. ring.	sclerotic ring.
s. fr.	split fin-rays.
so.	probably a supraorbital bone.
sp.	position of spiracle.
sscap.	suprascapula.
temp.	temporal.
v. edge	ventral edge of bone.
vert.	dorsal vertebral elements.
v.s.r.	ventral scale row.



1 2 cm.



2 1 cm.

3 2 mm.

Saurichthys striolatus (Bronn).

1 2 cm.

2 2 cm.

Saurichthys curioni (Bellotti).

THE BREEDING BIOLOGY OF EQUATORIAL VERTEBRATES: REPRODUCTION OF THE BAT *CHAEREPHON HINDEI* THOMAS AT LATITUDE 0° 26′ N.

BY

A. J. MARSHALL

Department of Zoology and Comparative Anatomy, St. Bartholomew's Medical College, University of London

AND

PHILIP S. CORBET

*East African Fisheries Research Organisation, Jinja, Uganda**

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(With 2 figures in the text)

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INTRODUCTION

A distinct breeding season has been demonstrated in at least three species of tropical mammals. In the extremely equable climate of Espiritu Santo (15° 15′ S.) Baker & Baker (1936) reported that the fruit-bat *Pteropus geddiei* usually parturates from August to September after copulation during autumn in accordance with the general tendency in fruit-bats, deer and sheep. In the same latitude Baker & Bird (1936) further reported that the insectivorous bat *Miniopterus australis*, spending most of each day in a dark, almost thermostatic cave, nevertheless has one of the sharpest breeding seasons known. Most of the females became pregnant in the first few days of September (in " spring ").

A study of the fruit-bat *Pteropus giganteus* was made much closer to the equator at 7°N. in Western Ceylon by Marshall (1947). Again a very sharp sexual season was shown. In two successive years conception occurred in December, shortly before the days begin to lengthen. Specimens taken ten years later in the same area had a similar conception date and so proved that

* Present address: Virus Research Institute, Entebbe, Uganda.

the sexual cycle of at least one seasonally breeding tropical animal is annually recurrent (Marshall, unpublished).

The two first-mentioned studies were carried out as part of the work of the Oxford University Expedition to the New Hebrides of which one of us (A.J.M.) was a junior member. In his final paper on the reproduction periodicity of vertebrates at 15° 15′ S., Baker (1947) concluded that the data strongly suggested that the breeding seasons there are controlled by " environmental factors of a totally unsuspected kind, not affecting the sense organs or meteorological instruments of Man ".

Although all three studies cited above were carried out in the tropics, it is nevertheless not impossible that day-length changes might control the sexual periodicity of the mammals involved. The present report concerns an investigation of the reproduction of a mammal existing almost on the equator where the difference between the longest and shortest days (*ca* two minutes) is presumably too slight to influence the neuroendocrine mechanism of any vertebrate. Here, on the northern shore of the Victoria Nyanza at Jinja (altitude 3878 feet) there is little variation in temperature and humidity and, although there are said to be " wet " and " dry " seasons, rain nevertheless falls throughout the year (Table 1), and the environment remains lush.

MATERIALS AND METHODS

Chaerephon hindei is probably the commonest of the East African free-tailed Microchiroptera. It occurs in enormous numbers around the shores of the Victoria Nyanza. At Jinja, the place of our collections, it congregates in such numbers in European and Indian dwellings that it is sometimes necessary temporarily to vacate houses while the accumulated guano is removed from their ceilings. Such unlimited supplies of *C. hindei* made the species ideal for the present investigation. All material used (211 males and 224 females) was collected from the ceiling of the East African Fisheries Research Organization laboratory.

The monthly samples were collected by an African laboratory attendant who went into the roof and plucked the bats with long forceps from crevices in which they took refuge. Collecting was found to be most successful during very early morning when the bats were relatively somnolent. The bats were killed with chloroform and a ventral incision was made before they were preserved in formalin.

At the end of fifteen successive, approximately mid-monthly, collections the preserved animals were examined for maturity, pregnancy and stomach contents. The modal fore-arm length was 38 mm. but that of a few bats was almost 39 mm. No gravid female, or male with spermatozoa, possessed a fore-arm less than 37·5 mm. long.

The uterine horns of insectivorous bats are so minute, and the endometrial reaction is so pronounced, that pregnancy is readily detected macroscopically. In each month's sample the females with a swollen uterine horn were set aside and the diameter of the gravid horn was measured. The testes of the mature males were taken to London and sectioned to determine whether seasonal variations in spermatogenetic activity occurred.

TABLE 1

The Jinja Climate

Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
					*Mean rainfall**						
2·02	2·88	4·90	6·83	5·27	2·49	2·03	4·07	3·25	3·87	4·00	3·31
					*Number of days of rain**						
7	7	11	16	17	9	7	11	11	10	11	8
					Mean maximum temperature†						
84·7	84·6	83·5	81·7	80·2	79·9	79·5	80·6	82·2	83·4	83·3	83·2
					Mean minimum temperature†						
64·0	64·7	64·9	65·0	64·5	63·6	62·2	61·9	62·7	63·7	64·0	63·7
					Mean relative humidity†						
77	80	82	83	85	84	87	85	83	78	76	76

* Calculated over a period of 43 years

† Calculated over a period of 14 years

The rainfall records used in Fig. 1 were obtained from the Research Organization gauge within 100 yards of the point where the bats were collected.

OBSERVATIONS

The preliminary examination of adults collected during 1955–56 revealed pregnancy ratios as shown in Table 2. To infer from these figures that the sex ratio is approximately unity and that about 37 per cent of the female population is generally pregnant is not necessarily valid since we had no way of discovering whether or not our collecting was selective. Pregnant females may have been more readily caught. However, whether or not collecting was biased, it is a fact that substantial reproduction occurs in every month of the year.

TABLE 2

Incidence of pregnancy in monthly samples of *C. hindei*

Date	Total	Male	Female	Pregnant	Percentage pregnant
1955					
10 July	11	5	6	1	17
14 August	48	12	36	12	33
14–15 September	33	9	24	14	58
16–18 October	21	12	9	2	22
16–17 November	28	19	9	3	33
19–20 December	26	14	12	2	17
1956					
16–17 January	34	15	19	6	32
21 February	30	13	17	9	53
15 March	26	16	10	5	50
12–13 April	22	8	14	4	29
15–16 May	35	21	14	4	29
15–17 June	27	15	12	5	42
15–17 July	30	19	11	1	9
14 August	35	19	16	10	63
15 September	29	14	15	5	33

There was unmistakable evidence too, that within the general pattern of continuous reproduction there were groups of females in reproductive synchronization. Judged by the relative uniformity of the size of the embryos in three of the monthly samples, it would appear that numbers of females come into concerted oestrous and are fertilized at about the same time. Thus, of the fourteen pregnant bats taken during September 1955, all embryos except one were of strikingly similar size. In the following February, seven embryos of nine pregnancies were again of a remarkably uniform size. These were apparently at full term. In August 1956, too, the various embryos were all of fairly constant size.

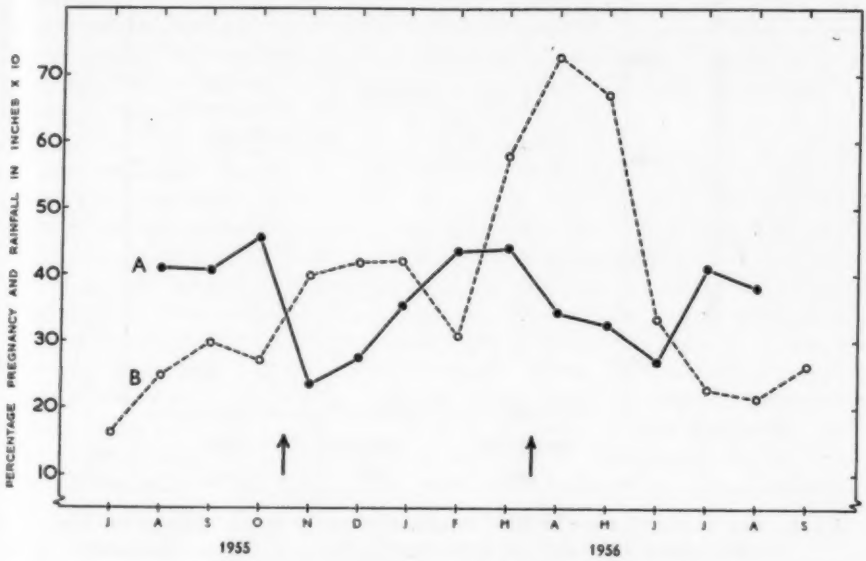

Fig. 1.—Pregnancy of *C. hindei* in relation to rainfall at Jinja during 1955–56. A : per cent of females pregnant per month. B : rainfall per month. Results have been smoothed by a 3-month sliding mean. Arrows mark the times at which the per cent pregnancy dropped abruptly. Marks on the abcissa indicate the mid-point of each month, this being the time at which collections were made.

Daylength, temperature and humidity (Table 1) are almost certainly too unvarying to be responsible for the minor breeding synchronization observed. Rainfall, on the other hand, fluctuates to a greater degree. Although there is rain in every month of the year, two " wet " seasons are recognised, the first in March–April, and the second in October–November. Rainfall values during the period of observation (Table 1) do not show very large differences in monthly precipitation at either of these two times. However, the position of Jinja in relation to the inter-tropical convergence zone provides grounds for expecting that the annual peak dates will occur fairly regularly at such times (see Manning, 1957). It was thought, therefore, that the fluctuations observed

in the proportion of pregnancies, and also their occasional synchronization, might reveal possibly, a correlation with local rainfall. The appropriate records are plotted in Fig. 1, both rainfall and pregnancy data being expressed as 3-month sliding means in order to minimize the effects of relatively small samples.

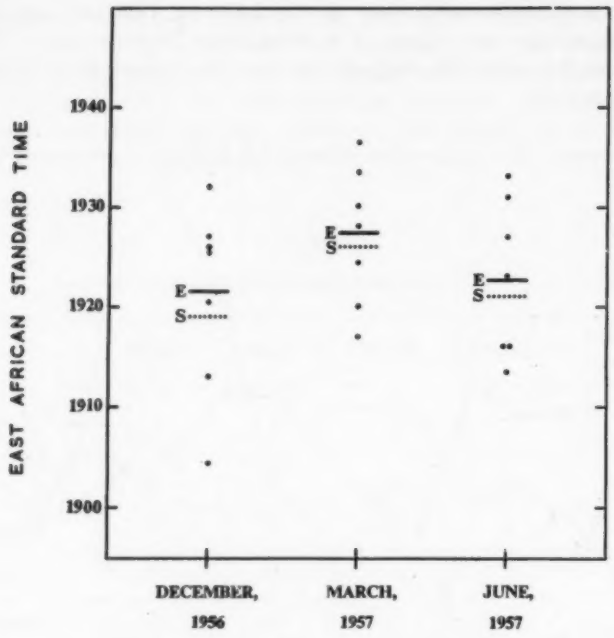

Fig. 2.—Exit times of *C. hindei* at Jinja, in relation to time of sunset. Each of the three series of observations was made over seven days from 18th to 24th of each month. In the diagram each dot represents one day's observation. E : average exit time. S : 30 minutes after average sunset time.

Throughout the year the stomachs of adult bats contained abundant insect material. This was usually too macerated to be identified specifically, but the remains of Chironomidae, Chaoborinae, and to a lesser degree Coleoptera and Hymenoptera, were well represented. The young bats contained coagulated milk. Those with a fore-arm length of 37·5 mm. contained, irrespective of season, a mixture of milk and the remains of large cockroaches (*Leucophaea* sp.). No cockroach remains were found in stomachs of adult bats. These insects, which attain a length of over 60 mm., are extremely common in the ceilings in which the young hang, and it is probably there that they are caught.

The importance of chironomid and caoborid Diptera as food for the adult bats is of interest in connection with seasonal fluctuations, because there is some evidence (e.g. Carpenter, 1920) that these insects may be more abundant

(or at any rate more " available ") during the wetter periods of the year. It may therefore be of adaptive significance that the greatest numbers of young appear to be born at the times of peak rainfall. However, it must be emphasised that before any causal sequence can be postulated, namely : rainfall/abundance of principal food/reproduction, a far more extensive series of observations and a precise knowledge of the length of gestation, are essential. Among the Microchiroptera there is a great variation in the duration of gestation : it varies from 44 days in *Pipistrellus pipistrellus* (Deanesly & Warwick, 1939) to more than five months in *Desmodus rotundus* (Wimsatt & Trapido, 1952).

That individuals (as distinct from the population) of *C. hindei* do not reproduce continuously was suggested by observations on the males. In many adults one or both testes were intra-abdominal. In some cases, where both organs were retracted, spermatogenesis had ceased. All males with a fore-arm longer than 37·5 mm. possessed some spermatozoa in their epididymides, irrespective of the current location of the testes.

In the course of this study, it was thought worthwhile to see if there was a close correlation between the time of sunset or local light intensity and the time when the bats began to leave the roof in the evening. Exit time was defined as that at which the first ten bats were seen to have left the roof. Observations of exit times and light intensity were made by Mr A. Tjønneland on each night of three separate weeks in the year, the weeks having as their centre-points two solstices and an equinox. The results give no evidence of any close correlation existing between light intensity and the exact time of evening emergence : during the three separate weeks, the geometric means of light intensity at exit time were 0·059, 0·060 and 0·092 lux, although intensities varied from 0·007 to 6·500 lux. There is, however, a clear suggestion that exit time is constant in relation to sunset (Fig. 2), the average being 31 to 32 minutes after sunset during both solstices and also at the March equinox. This may be indicative of an endogenous rhythm.

DISCUSSION

The above observations indicate that *Chaerephon hindei*, living in an environment where fluctuations in day-length, temperature and humidity are negligible, and where rainfall is not restricted to one or two periods in the year is able to dispense with a breeding season and reproduce, the whole year round. Wimsatt & Trapido (1952) too, report that the tropical American Vampire Bat (*Desmodus rotundus*) appears to be without season in the Panama Zone at *ca.* 9° N. Another small tropical mammal which is apparently aseasonal is the Multimammate Mouse (*Mastomys erythroleucus*) of Sierra Leone (*ca.* 8° 30′ N.) (Brambell & Davis, 1941).

That reproduction may begin at a very early age is suggested by the observation that, although the modal fore-arm length in adults is 38 mm., females can become pregnant with a fore-arm length of a fraction over 37·5 mm. at which size some individuals are still being suckled. The high ratio of pregnancies strongly suggests, but does not prove, that individual females parturate

more than once a year. All adult males possessed mature epididymidal spermatozoa irrespective of the month of collections although they did not undergo continuous spermatogenesis. Bats are rarely polyoestrus, but the data of Matthews (1941) suggest that the African *Nycteris luteola* is probably so during its breeding season. Wimsatt & Trapido (1952) report that the tropical Vampire Bat also appears to be polyoestrus.

Proof of the absence of annual periodicity in the present species at 0° 26′ N. inevitably leads to a reconsideration of factors that might be responsible for the precise timing of the cycle of the allied cave-dwelling microchiropteran *Miniopteris australis* at 15° 15′ S. in the New Hebrides (Baker & Bird, 1936).

In Santo the diurnal movements of *M. australis* were apparently influenced by light. Regular observations were not made, but some evidence indicated that at about 20 minutes before sunset bats start to fly about within the cave. About 10 minutes before sunset their emergence begins and then continues until 10 minutes after sunset. Thus, the population of perhaps about 5,000 leaves the cave whilst it is still light (but with the cave entrance in the rainforest becoming dark). These bats are replete and almost all back in the cave by 2 a.m. and so it can scarcely be thought that their cycle is " timed " by the dark period. However, if we assume that an appreciable proportion of the population hangs sufficiently close to the cave entrance, it is perhaps possible that the breeding cycle may be influenced by photoperiod. Alternatively, it might be assumed that the Santo *Miniopterus* become active at the same time each evening in response to an endogenous clock-like timing mechanism (see review by Pittendrigh & Bruce, 1957). The actual sexual cycle might still be regulated by photoperiodicity.

In the years 1933–34 the females of *M. australis* became pregnant in the first days of September ; and it is believed that the cycle is annually recurrent. At 15° 15′ S. the difference in daylength between the " winter " solstice (21 June) and 1 September is about 21 minutes. By the latter date day-length is increasing by two minutes every day. It has not yet been proved that bats are susceptible to photostimulation. If, indeed, they are, then it is not impossible, perhaps, that the cycle of *M. australis* is under such control. The sexual cycles of north temperate zone passerine birds are usually held to be under photoperiodic control. Yet the British Robin (*Erithacus rubecula*) begins its sexual cycle in the foggy English midlands in the first days of January when the days are only 14 minutes longer than at the winter solstice and when (on January 7) the daily increase is of the order of 1·5 minutes.

If the cycle of the temperate zone Robin is " timed " by photoperiod it is possible that that of tropical (but not equatorial) bats is likewise. The remarkable sexual synchronization of the whole colony of cave bats is as striking as that of many species of colonial birds. Unfortunately, in Santo, we did not locate and investigate at conception time other bat colonies in order to see if, like groups of birds, they were somewhat out of phase with each other.

The question of photoperiodic control of the sexual cycle of fruit-bats may be less complicated, for these animals hang all day in the sunny upper strata of the forest. In Santo copulation by *P. geddiei* began in February,

but the season is relatively prolonged since embryos less than 1 gm. in weight were found in June or July. *Pt. geddiei* follows the general tendency of fruit-bats (shared by sheep and deer) to copulate during decreasing daylength. Bissonnette (1941) and Yeates (1949) have shown experimentally that the sexual cycles of goats and sheep respectively can be modulated in temperate zones by the régimes of decreasing day-lengths. As the cycle of *Pt. geddiei* appears to be annually recurrent, perhaps the only outstanding question is whether the species can appreciate the annual decrement of 11 minutes between the " summer " soltice of 21 December and 1 February (when day-length is decreasing by about 30 seconds per day and when the females begin to come into oestrous). It is relevant at this point to mention the recent work of Norris (1958), who has shown that in *Nomadacris septemfasciata* Serv. (Orthoptera, Acrididae) diapause is induced at about 7°S. during March, when the daily decrement in daylight is equivalent to slightly less than 30 seconds. This, however, appears to be the only example known of an animal possessing so refined a response to changing day-length. Baker & Baker (1936) suggested that decrease in day-length and amount of ultra-violet light may be important in controlling the onset of the copulatory period of *Pt. geddiei*, but this idea was subsequently abandoned (Baker, 1947).

In the case of the Ceylonese *Pt. giganteus*, there is no doubt that the cycle is precisely recurrent. The question here is whether or not at 7°N. the animals can be influenced by the substantial light decrement of some 69 minutes that occurs between the " summer " solstice on 21 June and 1 December. In the years 1936, 1937 and 1947 (Marshall, unpublished) copulation occurred just after the latter date.

Studies of fruit-bats living almost precisely on the equator are much needed to discover whether, divorced from the possible influence of the change from increasing to decreasing day-length, such animals behave as does *C. hindei* or whether, perhaps, they retain a breeding cycle governed by the periodic appearance of a food crop or other external stimulus.

SUMMARY

1. The insectivorous bat *Chaerephon hindei* breeds prolifically throughout the year near the equator at Jinja (lat. 0° 26′ N.) on the northern shore of the Victoria Nyanza in Uganda.

2. There is here little variation in temperature and humidity. Rain falls throughout the year, the environment remains lush and insect food is plentiful.

3. Various data suggest a high breeding rate. Further, reproduction probably begins at a very early age since, although the modal fore-arm length in adults is 38 mm., females can become pregnant with a fore-arm length of a fraction over 37·5 mm. at which size some young individuals are still being suckled.

4. The epididymides of all mature males contained spermatozoa irrespective of the month of collection. Investigation of intra-abdominal testes however, showed that spermatogenesis is not continuous all individuals.

5. Within the general pattern of continuous breeding within the colony, groups of females were in reproductive synchronization.

6. There is a clear suggestion that the evening time of exit is not related to light intensity but is constant in relation to sunset. The average time of exist was 31 to 32 minutes after sunset during both solstices and also at the March equinox. This may suggest the operation of an endogenous diurnal rhythm.

7. The possibility of photoperiodic control of breeding seasons of tropical, excluding equatorial, bats is discussed and affirmed.

ACKNOWLEDGMENTS

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THE BREEDING BIOLOGY OF EQUATORIAL VERTEBRATES: REPRODUCTION OF CORMORANTS (PHALACROCORACIDAE) AT LATITUDE 0° 20′ N.

BY

A. J. MARSHALL

Department of Zoology and Comparative Anatomy, St. Bartholomew's Medical College, University of London

AND

J. D. ROBERTS

East African Fisheries Research Organisation, Jinja, Uganda

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(With 1 figure in the text)

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INTRODUCTION

Despite widespread speculation concerning the external factors that may influence the sexual cycle of equatorial animals, there has been up to the present no study of the breeding cycle of any bird existing on or even very near the equator. Moreau (1931, 1936), Lack (1950), Voous (1950) and others have assembled data indicating that many tropical species possess definite breeding seasons within at least 5° 30′ of the equator and Baker, Marshall & Harrisson (1940) proved that at 15° 15′ S. the New Hebridean passerine Golden Whistler (*Pachycephala pectoralis*) has a sexual season as sharp as that of most birds living in temperate zones. Chapin (1954) on the other hand, confirmed previous observations that the Sooty Tern (*Sterna fuscata*) of Ascension Island (lat. 7° 55 S.) is not an annual breeder and that, in fact, it reproduces five times during every four year period. Closer still to the equator, at latitude 3° 12′ N. in Columbia, South America, Miller (1954) reported that of ten selected species living in a relatively equable area, eight bred or were " in physiologic readiness for breeding " throughout the year and that the remaining two species showed " well ordered annual cycles ". Of the two cyclical breeders, one bred before and during, and the other after, an annual period of increased rainfall.

The nomadic Red-billed Weaver-finch or Dioch (*Quelea quelea*), which in arid parts of Tanganyika and Kenya oscillates back and forth across the

equator in relation to food supply, has been studied by Disney & Marshall (1956). Although this species is experimentally susceptible to photostimulation (Marshall & Disney, 1956), it breeds at any time of the year after the appearance of long green grass that follows rain-fall (Marshall & Disney, 1957).

The purpose of this and another study (Marshall & Williams, 1959) was to investigate the reproductive cycles respectively of " stationary " and migratory species that live almost on the equator and in an area, moreover, where little variation is manifest in temperature, humidity, rainfall or seasonal food supply.

MATERIALS AND METHODS

The White-throated Cormorant (*Phalacrocorax carbo lugubris* (Rupp.)) and the Reed or Pygmy Cormorant (*P. africanus* (Gmelin)) exist in great numbers on the Victoria Nyanza. The former feeds in the deeper water, sometimes out of sight of land, whereas the smaller animal rarely ventures far from the shore. Thus the two do not compete for food, and they nest side by side without conflict in waterside ambatch trees on the same islets. In close association with the two cormorants there breeds also the African Darter (*Anginga rufa*) and the Little Egret (*Egretta garzetta*) and, in the lower foliage of the same and nearby vegetation, the Golden Weaver (*Xanthrophilus aurantius*). The two cormorants were chosen for study because they are so conspicuous that it was easy to be sure whether they were in fact breeding at any given period. A second reason was that local residents, including naturalists, categorically declared that both species " breed all the year round ".

The present investigation is based on observations of proved breeding colonies over an almost continuous period of nineteen months, during a specific check-period a year later, and on the laboratory examination of the gonads of seventy-seven birds taken in all except three months of the year.

BREEDING ECOLOGY

The northern reaches of the Victoria Nyanza are besprinkled with islands, most of which are heavily timbered close to the shore and apparently ideal nesting places for the vast population of cormorants that inhabit the lake. Yet surprisingly, these birds (as well as the darter and egret) regularly build (in the area shown in Fig. 1) in four places only. The two largest northern breeding grounds are Mpuni Island and Ekunu Island in the lake. Secondly, building occurs on two small adjacent Nile islands at Ripon Falls (now converted into meagre rapids by the rise of water occasioned by the newly constructed dam). Thirdly, between Ripon Falls and the dam there protrude from a recently drowned islet four trees that are covered with nests. (It is almost certain that these trees will rot and disappear). Fourthly, about 1·5 miles below the dam there dwells a permanent colony on one of a string of islands that stretch across the river. To and from all these Nile breeding islets flight-lines lead along the lake each dusk and dawn. It was thought possible that additional colonies might exist farther down the Nile, so one of us flew about fifteen miles down-stream and proved that no such colonies in fact occur.

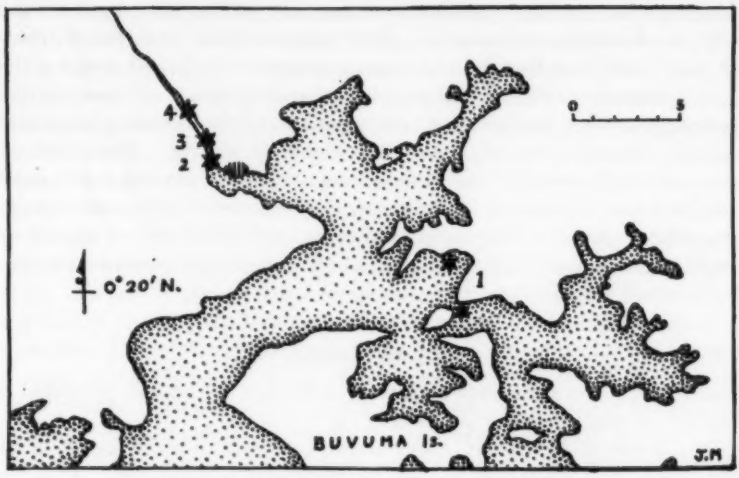

Fig. 1.—Breeding sites of Phalacrocoracidae in northern Lake Victoria and the Nile head-waters during 1955–57. The stars near the figure 1 indicate the positions of Mpuni (lower) and Ekunu islets. For explanation of the three other indicated areas, see text. The cross-hatched area shows the position of Jinja.

Several other colonies were located outside the area mapped (including one on an almost treeless rocky islet), but only on two occasions anywhere were nests discovered on a large island. The first exception noted was a colony of about 300 nests built in August in Pilkington Bay (of Buvuma Island) after the Mpuni Islet colony had deserted due to incautious preliminary collecting activity by ourselves. This splinter colony packed their 300 nests into three big ambatch trees growing slightly off-shore. Egrets, darters and golden weavers also joined the new community. Although the nest-trees were growing in lake-water, the nests were accessible, via branches, from the shore. Soon the whole colony of water-birds deserted their nests, leaving the eggs exposed and unprotected. The second exceptional colony was established in the same bay in December. It was very small and contained only fifteen nests. These, and their eggs, were deserted during the following month.

Thus, the only two colonies known to be established away from tiny islets failed to produce young. We are sure that large adventitious colonies could not have been established in the area without our knowledge. Even a moderate-sized colony of 300 nests soon comes to interrupt the green shore-line with a white patch recognizable a mile away.

The emphatic preference for small islets is obviously governed by predator pressure within the area. Although one large monitor (*Varanus niloticus*) was found on Mpuni Islet, serval cats and other predaceous carnivores do not reach such islets. However, if the cormorants restrict their nests to the very few tiny islets that are available, it follows that only a small proportion of the total population can breed at any given time.

Perching near nesting islets at various parts of the lake were often large flocks of non-breeding cormorants. Five mature adults were taken from such groups and each was found to contain moderately enlarged oocytes (largest 9 mm. in diameter) or very small bunches of spermatozoa. These groups were in physiological readiness to take over segments of the breeding islets as these successively became vacant after the flight of young. That this indeed happens was indicated by the differential stages of development shown in every big colony. Thus, at any given period an islet would contain segments of nests with fresh or slightly incubated eggs, heavily incubated eggs or downy nestlings, large young about to fly—or, of course, groups intermediate between those described above.

OBSERVATIONS

Observations were confined to Mpuni and Ekunu, the two principal breeding islands on the lake near Jinja (Fig. 1).

Mpuni is essentially a dry rocky outcrop about 80 × 50 yards in extent. It rises gently to a height of ten feet or more above lake-level. It is covered by *Triumfetta*, a broad-leaved, yellow-flowering evergreen, the undergrowth of which is densely tangled and decked with purple convolvulus (*Ipomea*). Irregularly dispersed around the islet are ambatch trees (*Herrminiera*) in which nest cormorants, darters, odd egrets and golden weavers. At times at least 700 nests are present. Those of the Pygmy Cormorant slightly predominated on the two occasions when counts were made, even though the pied bird appears to be much the commoner of the two on the lake. Many nests are built within a foot or so of the water. Sometimes they touch each other.

There seemed always to be room for a greater number of nests than were built at any one time. Nests were never built in isolated ambatch trees: the birds were emphatically colonial and thus always mutually protective. Some trees contained as many as thirty nests. Terns, odd waders, small crocodiles, a *Varanus* and a black snake shared the rocky wooded shores. The cormorants nesting in the ambatch were usually without shade and almost fully exposed to the weather.

Ekunu, on the other hand, is a very slightly elevated, patch of sometimes barely dry earth about 50 × 30 yards in extent* that is almost surrounded by ambatch and otherwise covered in parts by small thickets of shrubs and creepers. The total vegetation covers three or four acres. At one end of the island there is considerable swamp of ambatch that allows an enormous focus of nesting cormorants, with many darters, and some egrets and odd Night-herons (*Nycticorax nycticorax*). The ambatch also shelters numbers of Black Crakes (*Limnoirox flavirostra*) that are partly scansorial : they even run over creepers although they are of course basically terrestrial. According to Bannerman this crake even breeds aloft around Lake Victoria. This surprising

* Consequent upon the *artificially-induced* rise in lake-level (see p. 618) the island is rapidly changing. The area of dry land is now restricted to about five square yards, in addition to a few massive slabs of rock that may soon be the only dry land.

habit may be an adaptation to escape *Varanus*. The island is almost surrounded by reed-beds and Jacanas (*Actophilornis africanus*) run on the lily-leaves in the tiny lagoon between reeds and ambatch. Catfishes (*Clarias*) come inshore in shoals to feed on fish dropped by the cormorants and odd lungfishes are found in the Nile cabbage (*Pistia*) in the swampy sections between land and ambatch. At least 800 cormorants nests were found on each occasion (in successive Septembers) that counts were made. Those of the less plentiful Pygmy species appeared to be in the majority. (The opposite was the case on the islands in the Nile). As on Mpuni, there were present all stages from fresh eggs to young that were big enough to flutter from the nests on our approach. In many places nests were crowded into " slums ", with corpses hanging out of those occupied by healthy young. Some nests were built on such insecure and rotten old sticks that they had been tilted, with the imminent loss of eggs, merely by the weight of the guarding parent.

It was planned in the first instance that observations by one of us (J. D. R.) on the island colonies should extend in fortnightly periods from July 1955 until the same time the following year. Pressure of routine duties precluded precise population counts from being made. However, each fortnight a launch was brought close to the ambatch so that the contents of many nests could be observed. Only when *eggs or young were actually seen* were the species recorded as breeding.

From July 1955 until January 1956 both species of cormorants, and the darter, nested in profusion. During each month, too, egrets were seen on their nests. There seemed to be every indication that here were equatorial species that did in fact " breed all the year round ". Then late in January, each island was deserted except for odd groups of roosting birds. During February, March and April the islands were almost deserted, but in mid-May they were again populated and building activity was observed. In the first weeks of June *P. carbo* were incubating on both islands and in the following weeks *P. africanus*, the darter and the egret all started to sit on eggs. Thus breeding was again at full pressure by the end of the first twelve months' observations.

There was no suggestion that any man-made disturbance had caused the birds to abandon their colonies. At the same time, it seemed obvious that some kind of external inhibitor had operated. It was inconceivable that the whole vast population of each species, possessing " staggered " breeding cycles, had exhausted its sexual potential at the same period and had been compelled to leave both islets empty for the same four months of the year.

It became necessary to continue observations at least until January 1957, to discover whether breeding would be continuous until that date, and whether reproduction would then stop at the same time as in the previous year. This was, in fact, precisely what did happen. The station launches were out of commission from 9th November until 11th January but in both the first and last half of January each species of cormorant, and the darter, had young. However, only a few nests on each island now contained eggs or newly hatched chicks. Hundreds of well-grown cormorant chicks (but no young egrets) were being fed, and by the second half of February all the nests were again

empty and deserted. During the first half of April, when our observations had to be ended, the islets were still occupied only by roosting birds. In order to make absolutely certain that the stoppage is recurrent, check observations were made during the early months of the *third* successive year (1958). Reproduction was nil on both islands, and the first eggs after the renewal of breeding were seen on 23rd May.

The incubation period of cormorants is about twenty-eight days and the young remain in the nest for more than thirty days. Therefore, it follows that in three successive years the birds inhabiting the two most populous nesting islets in our area stopped laying in December.

Two obvious questions had to be asked :

1. Does any climatic factor detrimental to the safety of nest and eggs come seasonally into operation during December–January and,

2. Is there any seasonal failure in food supply at this period ?

The second question was easily answered in the negative. Nestlings of all sizes were dissected and found to be engorged with *Haplochromis* between 60 and 80 mm. long together with unidentified cichlid remains that were again probably those of *Haplochromis*. These fishes are abundant throughout the Lake all the year round. Further, station fishing records showed that during the inhibitory period there was no suggestion of any failure in the food supply of the adults (chiefly *Haplochromis*, sometimes *Tilapia*, *Mormyrus* and *Bagrus*).

TABLE 1

Percentage distribution of wind velocities over 24 m.p.h. at Jinja

East Afr. S. Time	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June
0830 hours	—	—	—	2	5	5	5	1	3	4	1	1
1730 hours	12	7	8	10	8	9	19	31	13	13	11	4

The Jinja weather is tabulated briefly by Marshall & Corbet (1959). Analysis of such records at first sight showed no factor that might inhibit reproduction. However, a consideration of seasonal wind velocities (Table 1) perhaps may provide the answer. The exposed, relatively flimsy nests must be highly vulnerable to the squalls which from time to time sweep over the Victoria Nyanza. Such storms, which are characterised by high winds and lashing rain, have at times destroyed relatively large vessels. The nests of cormorants, in brittle ambatch sticks that occasionally collapse under the mere weight of parent and young, would be highly vulnerable to such storms which sometimes dislodge tracts of papyrus which float in " islands " out of the lake down the Nile. From the meagre data at our disposal (Table 1) November, December and January are seen to be the months most subjected to high winds. It will be seen too, that in May, the months in which breeding restarted, there is a reduction in wind velocities and that this relatively placid period will now last until November.

In cormorants, like all birds so far investigated, the breeding time is probably dictated by the female (see Marshall, 1955). We believe it possible that these lake-dwelling species have evolved an inhibitory reaction to tempestuous conditions in the same way that ovulation in desert species is inhibited by relatively dry conditions even though the males, after a certain amount of rain, are often in full song and spermatogenesis. That at least some male cormorants were in fact in reproductive condition during the non-breeding period was shown by the presence of spermatozoa in two birds taken in February.

Again, of the females shot in May, the oocytes of two birds measured up to 5 mm. in diameter and those of a third were of a diameter no less than 20 mm., probably betokening preliminary activity. The velocity data in Table 1 relates to Jinja, the nearest meteorological station to the islands. Such shore data perhaps do not truly reflect the severity of the conditions obtaining from time to time out in the exposed body of the lake.

The velocity readings cited in Table 1 were made during daylight hours only and therefore may be to some degree misleading. Many lake storms develop between late afternoon and dawn and die away in the early morning. Therefore, even ashore, the months January to May are probably more tempestuous than would appear from the tabulated figures. Further, such records do not distinguish between a tempest that would devastate a colony and a mild squall at 25 m.p.h. that would perhaps do no damage whatever. At the same time it must also be considered that during May–July, the period in which reproduction again gets fully under way, there also develop night-storms that are not adequately recorded by morning readings.

DISCUSSION

The exclusively fish-eating cormorants *Phalacrocorax carbo* and *P. africanus* live in the relatively equable equatorial environment of Northern Lake Victoria in which food for both adults and young is abundant throughout the year. That pressure from terrestrial, customarily non-swimming predator(s) is heavy is indicated by the strong preference for nesting on small lake or river islets where the eggs and young are probably safe except for occasional attacks by monitors that find their way there.

The vast amount of available *Haplochromis* (fishes of little commercial importance) supports a large cormorant population. Yet because of the nesting conservatism mentioned above, relatively few cormorants can reproduce at any given time. Thus, each colony contains breeding groups that are in reproductive phase in themselves (e.g. all with newly hatched young) but which are out of phase with neighbouring segments of the colony (e.g. with fresh eggs or young almost ready to fly). As successive batches of young and their parents leave the colony, incoming groups take vacant possession, refurbish the battered nests, and ovulate. Examination of gonads gave strong indications that, as often claimed, these species breed all the year round. Had we merely taken a monthly series of specimens without actually observing the breeding colonies, we might have reported perennial reproduction.

The species are potentially capable of breeding the whole year round whereas in fact they do not do so : the islands are occupied for only eight months of the year. In three successive years ovulation was suppressed during December, at the beginning of the period during which relatively high winds sweep the lake, no doubt to the detriment of the flimsy nests in the brittle ambatch. In more sheltered parts of Lake Victoria breeding may indeed be continuous throughout the year.

It is suspected that individual pairs, and groups, of cormorants probably have sexual cycles not unlike that of the Sooty Tern (*Sterna fuscata*) of Ascension Island. This species lives in an equally fruitful, and perhaps even more equable, environment than the one under consideration and so the whole vast socially and sexually synchronized popu!ation of terns can breed successfully as soon as the post-nuptial refractory period has concluded and the new probably spontaneous, gametogenesis rhythmically occurs (Lofts & Marshall, 1958). Were the Ascension tern migratory, such a rhythm would carry it north into an unpropitious climate and natural selection would operate swiftly and disastrously (Marshall, 1951).

A totally synchronized, regular and rhythmical reproduction such as occurs in the Ascension tern seems to be prevented in the cormorants of Northern Lake Victoria by two important external inhibitors: 1, the relatively squally December–April period, and 2, the availability of very few safe nesting sites which in turn governs the number of birds that can nest at any given period. Groups of cormorants then, are in reproductive phase ; but the population as a whole is not. Until ringing work is carried out on a large scale there will be no means of knowing how often a given pair is able to reproduce.

SUMMARY

1. Reproduction phenomena in two colonies of water-birds were studied over an almost continuous period of nineteen months in the equable environment of the Victoria Nyanza at about latitude 0° 20′ N.

2. The cormorants *Phalacrocorax carbo* and *P. africanus* at first sight appear to breed all the year round, as is commonly stated, but in fact reproduce only from late May to December. A hiatus was proved to occur at the same period during three successive years.

3. The cormorants in the northern reaches of the lake breed only on wooded or occasionally rocky islets that are relatively inaccessible to predaceous carnivores. Segments only of each colony are in reproductive phase. As sections of the breeding isles are successively abandoned by young birds and their parents, fresh groups of sexually active adults move into vacant possession.

4. It is impossible that the whole population, which is not in reproductive phase, becomes sexually exhausted at the same period each year : some external inhibitor must operate to stop reproduction.

5. The environment is not subjected to marked fluctuations in temperature, or rainfall, and the food eaten by both adults and young remains abundant throughout the year. The only factor that seems likely to inhibit reproduction is the storms that sweep the lake between January and April. The islets on

which the cormorants build their flimsy nests are completely exposed. It is possible that they have developed an inhibitory response comparable with that which stops ovulation in xerophilous species during drought.

6. The species under review probably possess a sexual rhythm comparable with that of the Sooty Tern of Ascension Island but two factors – scarcity of safe nesting sites and an annually recurring period of unpropitious weather – prevent a totally synchronised regular rhythm of reproduction.

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THE DEVELOPMENT OF THE EUPHAUSIACEA (CRUSTACEA) ESPECIALLY THAT OF *MEGANYCTIPHANES NORVEGICA* (M. SARS)

BY

J. MAUCHLINE

*Marine Station, Millport and Department of Zoology, University of Glasgow**

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(With 4 figures in the text)

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INTRODUCTION

Ample historical surveys of the literature on the larval development of the Euphausiacea have been presented by Fraser (1936), Einarsson (1945), Gurney (1947), Heegaard (1948), and Sheard (1953).

The eggs of some euphausiids are shed freely into the sea, in others they are retained in egg sacs. Nauplii hatch from these eggs and these moult to a second nauplius stage followed by a metanauplius stage. The abdomen develops during the following three calyptopis stages, the third calyptopis larva having an abdomen with the full compliment of segments before it moults to the first furcilia stage. Fully developed pleopods are usually acquired in the first two or three furcilia stages but they can develop in several ways thus giving rise to the various forms of larvae within one stage. This variability of form is not confined to the earlier furcilia stages but is found throughout the later development. Early workers described each form as a stage and the first two furcilia stages were thus subdivided into eleven stages by Macdonald (1927 b).

Larval stages were also classified on the presence or absence of photophores, larvae with the full complement being known as cyrtopia stages, but this term is now obsolescent.

*Present address United Kingdom Atomic Energy Authority, R. & D. B., Biology Section, Windscale Works, Sellafield, Cumberland.

The work remained in this descriptive phase until Macdonald (1927b) suggested that the larvae in the Clyde passed through fewer stages than elsewhere. Rustad (1934) also found certain larval forms present in much greater numbers than others and his conclusions supported Macdonald's suggestions.

Fraser (1936) was the first to recognize clearly that each larva does not pass through each form found in the plankton but that there were certain dominant forms, the bulk of the larvae moulting from one dominant form to the next. He showed that non-setose pleopods became setose at the next moult and suggested that forms represented by small numbers of specimens in the plankton were variant forms.

A further advance was made by Einarsson (1945) who described and classified the various larval forms in the northern Atlantic.

Attention has been centred on pleopodal development in the early furcilia stages and the variation in the general morphology of the larvae has tended to be less considered since the work of Fraser and Einarsson. Heegaard (1948) and Bary (1956), however, have emphasized that the morphological characteristics of the larvae within each stage vary very much. Heegaard suggests that ecdysis and morphological development may be independent and hence larvae moulting into the next stage may not have the same morphological characteristics.

Sheard (1953), working with very large numbers of larvae of *Nyctiphanes australis*, clearly showed the various ways by which a larva of that species can attain the adult form. Consequently, he classified the larvae into three classes, furcilia I, II and III, in order to provide a basic nomenclature for comparing larval development in different species. His furcilia I comprised larvae with the eyes free of the carapace and the pleopods absent or present as non-setose rudiments ; his furcilia II comprised larvae with some or all pleopods setose and the pair of long lateral telsal spines unaltered at the base ; his furcilia III comprised larvae with all pleopods functional and the shape of the base of the long lateral spines altered.

In this work, new data on the larval forms of *Meganyctiphanes norvegica* in the Clyde sea area are presented. Lebour (1925) described the various larval forms of this species found at Plymouth and the larvae originating from the population of *M. norvegica* in Upper Loch Fyne were studied by Macdonald (1927b). Einarsson (1945) investigated the larval development of this species in the northern Atlantic. Heegaard (1948) described the early furcilia forms in the Bonnefjord and discussed the variations which he demonstrated in the morphological characteristics of larvae within one stage.

MATERIAL AND METHODS

The earlier larval stages were sampled by four fine townets so arranged on the warp as to fish the following depths simultaneously : surface, 50 m., 100 m., and 150 m. Four medium townets were substituted to catch the older larvae.

Samples were taken at least once a week in various regions of the Clyde sea area throughout the breeding season.

LARVAE OF *M. norvegica*

The larvae of *M. norvegica* have been classified into furcilia stages according to Einarsson's (1945) descriptions which were found to be accurate. Thus no detailed morphological descriptions of the larvae are presented here.

The calyptopis stages of *M. norvegica* were examined and the mean measurements, from the rostrum to the distal point of the telson excluding the setae, are compared in Table 1 with those presented by Lebour (1924), Einarsson (1945) and Heegaard (1948).

TABLE 1

	Lebour	Einarsson	Heegaard	Author
Calyptopis I	1·02 mm.	1·0 mm.	0·85 mm.	1·03 mm.
II	1·60 mm.	1·5 mm.	1·57 mm.	1·59 mm.
III	2·40 mm.	2·5 mm.	2·13 mm.	2·40 mm.

Personal measurements of the three stages are identical with those of Lebour and are very close to Einarsson's. Heegaard's measurement of the first calyptopis stage in Gulmarfjord is at the lowest end of the range in size

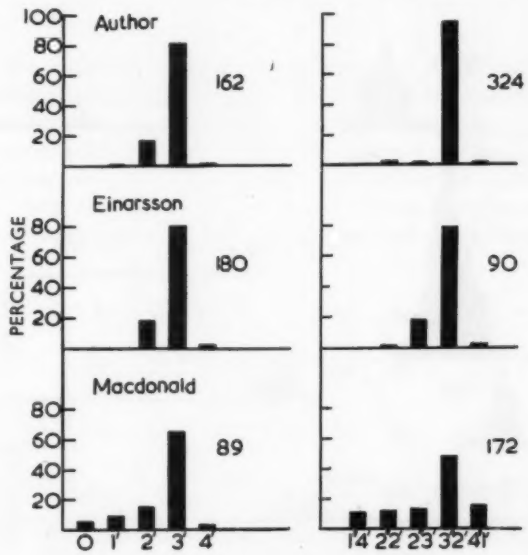

Fig. 1.—The frequencies, shown as percentages within each stage, of the various forms found within the first two furcilia stages of *M. norvegica* by Macdonald (1927), Einarsson (1945), and the author.
The sign ′ designates a non-setose pleopod ; the sign ″ designates a setose pleopod.

found in the Clyde. He measured only twelve calyptopis specimens and does not state how many of each stage there were but his measurement for the third stage is less than that of the smallest one found in this investigation, which suggests that his third stage larvae were indeed smaller.

The percentage incidences of the various morphological forms found in the first two furcilia stages were investigated. In order to compare these results with those of Macdonald (1927 b) and Einarsson (1945) the form with no pleopods has been included with those having non-setose pleopods. The furcilia II specimens are those with both setose and non-setose pleopods present. The percentages were calculated separately in both stages (Fig. 1).

The author's results for furcilia I are more like those of Einarsson than Macdonald. The form with two non-setose pleopods occurred later in the larval season which extended from the first week of April until mid-July. Three specimens with two, and 122 with three non-setose pleopods were caught before 13th May. On 13th May, however, twenty-four specimens with two and forty with three non-setose pleopods were found in the townettings examined. After the 13th, very few furcilia I and II larvae were caught in the Clyde sea area even though sampling continued every week until July.

The furcilia II results present a different picture from that of both previous authors. Macdonald found 52 per cent and Einarsson 21 per cent of the

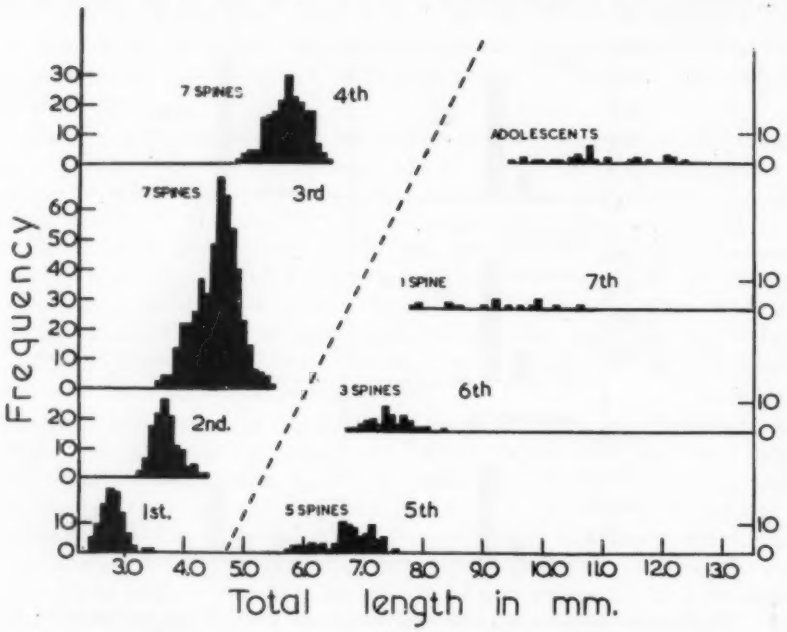

Fig. 2.—Length/frequency histograms of the furcilia stages of *M. norvegica*.

specimens in this stage varying from the dominant form. In the present investigation however, only 5 per cent of the total were variants.

The furcilia were classified according to Einarsson's descriptions, the range of measurements within a stage being shown in Fig. 2. Both the third

and fourth furcilia stages have terminal spines but in the third stage the endopod of the antenna is not segmented. The mean size of each stage is compared with Einarsson's measurements in Table 2.

TABLE 2

Furcilia	I	II	III	IV	V	VI	VII	VIII
Einarsson	3·0	4·0	5·0	6·0	7·0	7·5	8·0	8·5
Author	2·8	3·7	4·5	5·7	6·8	7·5	9·1	10·9

Einarsson does not state how many specimens of each stage were measured but it is most interesting that the increase in size at moulting seems to be relatively less in his later stages than in those here examined.

The mean sizes of the variant and dominant forms in the furcilia stages were calculated (Table 3) and the number of specimens of each form measured is shown in brackets.

TABLE 3

Non-setose pleopods				Setose and non-setose pleopods		
0′	2′	3′	4′	2″ 3′	3″ 2′	4″ 1′
2·76(1)	2·85(19)	2·85(83)	3·35(2)	3·65(5)	3·70(154)	4·0(6)

Later furcilia stages indicating number of telsonic spines.

7 sp.	7 sp.	6 sp.	5 sp.	4 sp.	3 sp.
4·5(446)	5·7(206)	6·0(1)	6·8(76)	7·7(1)	7·5(40)

Although the numbers are small, increasing size is associated with greater structural complexity. The specimen with four telsonic spines is an exception as it is larger than the mean size of those with three spines.

A similar correlation has been shown for various species by Sheard (1953) and by many other authors with fewer numbers of larvae available to them.

Heegaard (1948) thinks that the duration of each nauplius stage is three to four days, each calyptopis stage a little longer, and each furcilia stage about

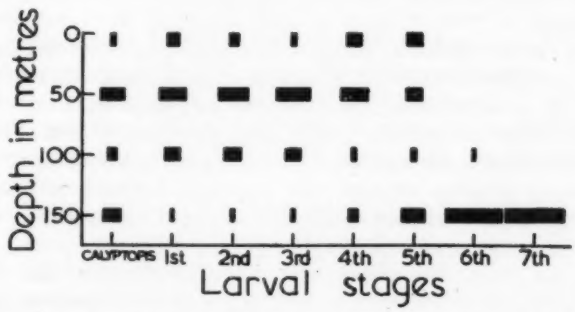

Fig. 3.—The vertical distribution of the different larval stages of *M. norvegica* in the sea during daylight hours. The sizes of the blocks are representative of the numbers caught at the various depths and times.

seven to eight days. In the present investigation each nauplius stage lasted three days and each calyptopis three to four days. No furcilia larvae moulted in the laboratory but from the continued sampling of the natural population the average duration of each stage is thought to be five to six days.

The vertical distribution of the larvae of *M. norvegica* in the sea during daylight hours was investigated (Fig. 3). All stages except furcilia VII and VIII were found from surface to bottom but the layer of greatest abundance was about 50 m. Furcilia VII and VIII lived much closer to the bottom than the rest and behaved more like the adults.

A diurnal vertical migration of the larvae takes place but since there are always larvae present in the surface layers it is not so marked as that of the adult.

The gut of the nauplius is not functional. Sars (1898) thought that the metanauplius feeds but Taube (1915) states that there is no connection between the mouth and mid-gut. Macdonald (1927 a) states that the gut is functional but he did not find food in it. A green mush, almost identical to the substance Macdonald (1927 a) calls flocculent detritus, was found in the stomachs of 10 per cent of the metanauplii here examined.

Vegetable detritus, a few diatoms, some filamentous algae and algal spores, fragments of dinoflagellates and mud particles were present in the gut of the larvae examined. Green mush was also present, more so in the earlier furcilia stages than the later ones.

A few of the furcilia VII and VIII specimens examined also contained crustacean remains.

DISCUSSION

When a crustacean larva moults it increases in size. If a large sample of the larvae of one species is measured and the results analysed on a length/frequency distribution a regular polymodal distribution is obtained. The increment of the modes at each moult is not usually constant but is always significant. If one larval stage, that is one mode, is missing or there is one too many then the curve becomes irregular in that region. Measurements of the larvae within a stage conform to a normal distribution on a length/frequency graph.

As already shown (Table 1) Heegaard's measurement for the calyptopis III stage of *M. norvegica* is smaller than that of other authors but this may be because there is an extra instar, the form with no pleopods, in the Gullmarfjord.

Heegaard refers to Lebour (1925) and Macdonald (1927 b) who found this form without pleopods and asks " . . . does (*sic*) the oceanic specimens of *Meganyctiphanes* develop without this stage at Iceland, whence Einarsson obtained his material, contrary to the development in the three other investigated localities with neritic specimens ? "

He suggests that Einarsson may have overlooked this form but if Macdonald's (1927 b, p. 790) results are examined it will be seen that he found only six specimens with no pleopods as compared with eighty specimens with non-setose pleopods, which suggests that the form with no pleopods was a variant form. The present author found one specimen (Fig. 1) and Lebour (1925) does not state how many she found ; her measurements of the calyptopis III larvae and the larvae with non-setose pleopods are identical to those found here so that it is unlikely that a distinct stage with no pleopods existed between them. It would seem, therefore, that the larvae

in Gullmarfjord are peculiar in having this form as a distinct larval stage.

Macdonald worked in Upper Loch Fyne and found a large number of variant forms in the first two furcilia stages (Fig. 1) whereas the author sampled lower Loch Fyne and the Firth of Clyde and found even fewer variants than Einarsson at Iceland. *M. norvegica* seems to have been more plentiful in Upper Loch Fyne in 1927 than in recent years and it may be that the environmental conditions have changed.

All the variant forms of the furcilia stages occurred in the plankton some time after the dominant forms were common. Whether food conditions or hydrographical conditions caused this is not known but Broad (1957) showed that the quantity and type of food available affects the frequency of moulting and the rate of development of larvae of *Palaemonetes pugio* and *P. vulgaris*. The frequency of moulting was found to be independent of the rate of development so that variation in form and frequency of larval stages arose.

It has been suggested that the oceanic conditions would be more uniform than the coastal ones and that this is why oceanic euphausiids have fewer variant forms within the larval stages. Einarsson showed that the degree of dominance of a form within a larval stage of *M. norvegica* varies at different stations and Sheard (1953) has presented even more conclusive results for *Nyctiphanes australis*.

Thus in order to elucidate the development of any one euphausiid species samples have to be taken throughout the whole period and area when and where larvae are present.

NOMENCLATURE OF EUPHAUSIID LARVAE

The nomenclature used to describe the larval development of the *Euphausiacea* is still a major problem. Sequential stages in crustacean larvae are usually associated with sequential moults but this is not so in the *Euphausiacea* unless the larval stages are named separately for each species.

It is now recognized that the number of larval moults in a species is not constant but that most of the larvae follow the same developmental path while the remainder pass through various numbers of moults. When several authors refer to the larvae of various species as " furcilia III " it is of advantage to know that these larvae are at comparable stages of development.

Sheard suggested that the furcilia larvae should be classified under the following headings :

Furcilia I Pleopods absent or present as non-setose rudiments.
II Some or all pleopods setose.
III All pleopods setose and functional.

If all calyptopis larvae moult to furcilia larvae without any pleopods then these form a distinct stage as they need another moult to acquire non-setose pleopods. This form is found in most of the *Stylocheiron* spp. (Frost, 1935 ; Lewis, 1955) and *Thysanoessa* spp. (Rustad, 1930, 1934 ; Einarsson, 1945) investigated. It may or may not form a distinct larval stage in *Nyctiphanes* spp. (Sheard, 1953 ; Boden, 1955). Therefore, it may be a larval stage in some species of a genus and not in others.

Heegaard (1948) records it as a distinct stage in the development of

M. norvegica in the Gullmarfjord whereas Einarsson (1945) at Iceland and Macdonald (1927 b) and the author in the Clyde sea area found it present only as a variant form. It seems, then, that there may be a variation within a species in the number of moults passed through by the greater percentage of the specimens when several sea areas are compared. This affects the numbering of the stages so that the furcilia I described by Heegaard (1948) does not have the same morphological characteristics as that described by Einarsson (1945).

In species which do not have a furcilia larva without pleopods the calyptopis III larvae moult directly to a form with non-setose pleopods. The number of pleopods present may vary from species to species or within a species. Usually, however, one form is present at a higher frequency than the others and this has been termed the " dominant form ". The non-setose pleopods in all larvae, whether derived from calyptopis III larvae or furcilia larvae without pleopods, acquire setae at the succeeding moult in all the species investigated.

It would seem of value, therefore, to group these larvae together as furcilia I and describe each form found, their range in size and numerical incidence.

A pleopod develops first as a non-setose rudiment which at the next moult acquires setae. The anterior abdominal segments acquire non-setose or setose pleopods first. That is, a furcilia I larva with non-setose pleopods usually moults to a furcilia II larva in which the non-setose pleopods are setose and the blank segments have non-setose pleopods. At the following moult all the segments have setose pleopods.

There are, however, exceptions to this. In *Nyctiphanes simplex* (Boden, 1951) the furcilia I larva with three non-setose pleopods usually moults to a larva with five setose pleopods. Where most larvae in furcilia II of a species have one or more of the posterior abdominal segments without pleopods and the most anterior segments have setose pleopods, two moults are required to produce a larva with five setose pleopods. This happens in the case of *Stylocheiron longicorne* (Frost, 1935), *Euphausia longirostris*, *E. spinifera* (John, 1936) and possibly in a few others. In other species, where this is not the normal path of development, a variable percentage of the larvae develop in this way and so have an extra moult.

The number of moults from the time a larva acquires non-setose pleopods until the pleopods become functional can thus vary. Sheard has ascribed all forms with setose and non-setose pleopods to furcilia II but has also included with them forms with five setose pleopods.

The larval form with five setose pleopods and the telsonic spines, usually seven in number, unreduced is the cause of some disagreement in the literature. *Euphausia* species (Bary, 1956 ; John, 1936) have only one larval instar with seven terminal telsonic spines and five setose pleopods. Boden (1951), however, suspects that there are several larval stages of this type in *Euphausia pacifica*. *Thysanoessa inermis* has three and *T. raschii* four consecutive stages (Einarsson, 1945) which have five setose pleopods and seven terminal

spines on the telson, the stages being identified by the comparative development of the thoracic appendages. *M. norvegica* has two such stages whereas *Pseudeuphausia latifrons* (Tattersall, 1936) has no such stage, the telsonic spines being reduced by the time the larva has five setose pleopods.

Boden (1950, 1951, 1955) has used the presence or absence of antennal endopod segmentation and the reduction sequence of the telsonic spines to classify the larvae of the species he investigated. In *Euphausia pacifica* about 40 per cent of the larvae with five telsonic spines and in *Nyctiphanes simplex* and *N. capensis* about 50 per cent of the larvae with three spines had the antennal endopod segmented. These seem to be valid stages judging by the measurements he presents.

The point, however, at which endopod segmentation takes place is variable when related to the telsonic spine reduction sequence in various species within a genus and differs very much from genus to genus.

In almost all euphausiid species, however, the sequential reduction of the terminal telsonic spines seems to be a constant feature although reduction occurs in various ways. The larvae with setose and non-setose pleopods usually moult to larvae with five setose pleopods and the telsonic spines not reduced in number. The known exceptions to this rule are *Pseudeuphausia latifrons* (Tattersall, 1936) and *Nematoscelis microps* (Gurney, 1947). The terminal spines may be reduced in number at the next moult (some *Euphausia* spp.) or as many as four successive moults may take place before the reduction begins (*Thysanoessa raschii*).

Therefore, considering all these facts it would be better to exclude all specimens with five setose pleopods and seven telsonic spines from furcilia II unless they were obviously derived directly from furcilia I larvae with five non-setose pleopods or their morphological characteristics made it obvious that they should be classed with furcilia II larvae. Instead, it is suggested that these larvae be classified by themselves as furcilia III and the number of instars, their form, incidence and size-range described.

There now only remain the larvae in which the telsonic spines are reduced in number. Various authors (Einarsson, 1945) have examined the possibility of using the lateral telsonic spines as characters for identifying the later furcilia stages but have concluded that there is far too much variation between species to make this useful.

Boden (1955) has criticized Sheard (1953) for ' lumping ' the late furcilia larvae together as furcilia III. He suggests that the concept of dominance is still useful and so they should remain separate and distinctly named. Sheard's including them together under one heading, however, does not obscure this concept as one provision is that the several instars should be described. One strong criticism made by Boden of Sheard is that his furcilia II larvae are distinguished from his furcilia III larvae by an alteration in the shape of the base of the lateral spines on the telson. This is certainly unsatisfactory and lends support to the suggestions made here.

The size range of larvae within a stage, which on a size/frequency histogram should conform to a normal distribution curve, should not decrease when

these larvae moult to the following stage. Instead, it should remain constant, according to theoretical mathematics, or according to some biological theories it should increase. In *M. norvegica* (Fig. 4) it remains almost constant until the instar with one telsonic spine when it increases by a half.

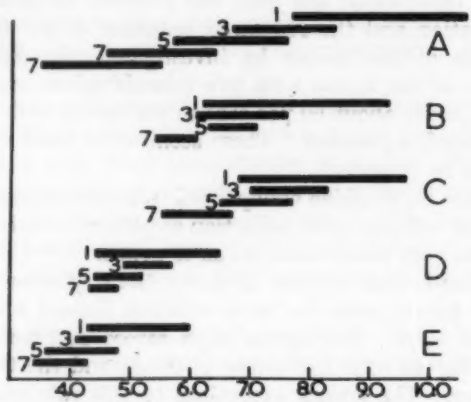

Fig. 4.—Size ranges of the larval stages of some euphausiids. A, *M. norvegica* ; B, *Euphausia vallentini* (John, 1936) ; C, *E. frigida* (John, 1936) ; D, *Nyctiphanes australis* (Bary, 1956) ; E, *N. australis* (Sheard, 1953).

The numerals at the left-hand side of the histograms refer to the number of terminal telsonic spines.

The range in size of the larvae of *Nyctiphanes australis* (Fig. 5, Sheard) with three telsonic spines is less than half that of larvae with five telsonic spines. Since there is a relationship between the size of a larva and its morphology the author would suggest that the larger specimens with five spines had them reduced to one at the next moult and thus omitted a three spine stage and that the three spine larvae Sheard found were derived from the smaller larvae with five spines. Sheard found that larvae with five telsonic spines did indeed have them reduced to one at the next moult. He also found that seven telsonic spines could be reduced to three in one moult and a similar explanation would fit this.

Bary (1956) with fewer numbers of larvae of *N. australis* did not find this decrease in size-range but the lower limit of the size range of larvae with one telsonic spine (Fig. 4) is much less than the lowermost limit of the supposed preceding stage. This seems to be a fairly common phenomenon (Fig. 5, *E. frigida*, *E. vallentini*) and would be explained if a number of the larvae omitted a stage in the telsonic spine reduction sequence.

The reduction sequence is 6–4–2–1 in *Stylocheiron suhmii* (Lebour, 1926) and there are very many species where the possible sequence is not known. Thus it is by no means obvious that the telsonic spine reduction sequence is a valid way of classifying the larvae. It would, however, be of value to classify these larvae together as furcilia IV and describe the dominant instars, their size-range and frequency.

CONCLUSIONS

No ideal larval classification can be devised for the Euphausiacea and consequently the most useful arrangement should be adopted. An attempt has been made in this paper to show that the larval development in the Euphausiacea can be divided into four phases.

In the first phase the calyptopis larva moults to a larva which either has or acquires at the next moult non-setose pleopods. There are thus either one or two moults in this phase depending on whether there is an instar without pleopods.

In the second phase the larvae with non-setose pleopods moult to larvae with setose and non-setose pleopods. In a few species there are larvae with five setose pleopods derived from a dominant furcilia I form with five non-setose pleopods and these should be included here and the situation made clear. Usually there is one moult in this phase but in a few species the first instar in this phase has one or two abdominal segments without pleopods ; this instar requires two moults to acquire five setose pleopods.

The third phase is characterized by the continued development of the thoracic appendages and the non-reduction of the terminal spines on the telson. The antennal endopod very often becomes segmented in this phase. The number of moults varies considerably, being one in some *Euphausia* spp. and four in *Thysanoessa raschii*.

In the fourth phase the terminal telsal spines are reduced and sometimes the " segmentation " of the antennal endopod takes place. The thoracic limbs continue to develop. The number of moults is questionable but is thought to be three. The sequence of the spine reduction shows some variation in different species and possibly within a species.

The author suggests that these phases be termed as follows :

Phase I	Furcilia I
Phase II	Furcilia II
Phase III	Furcilia III
Phase IV	Furcilia IV

Since the most important conception in our consideration of euphausiid development is that of " dominant forms " it must not be obscured. All the instar forms must be described and where there is much variation as many larvae as possible should be examined and measured. The measurements are very important and should be presented either as range of size within an instar, the mean size and number of specimens measured being indicated, or in the form of length/frequency histograms for each larval form or instar.

ACKNOWLEDGMENTS

I wish to thank Professor C. M. Yonge, C.B.E., F.R.S. and also the Director and Staff of the Marine Station, Millport for all the facilities made available to me. Special acknowledgment is due to the Skipper and crew of the research ship *Mizpah* who took samples for me in all weathers.

I would also like to acknowledge my receipt of a Fishery Research Training Grant from the Development Commission.

SUMMARY

The larval development of *Meganyctiphanes norvegica* in the Clyde sea area has been investigated and found to be different from that described by Macdonald (1927 b). The conclusion is reached that it can be divided into four phases, these being termed furcilia I, II, III and IV. A few notes on larval ecology are presented.

The facts required to elucidate the course of development in any one euphausiid species are discussed. It is pointed out that the environmental conditions appear to affect the development.

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FIELD IDENTIFICATION OF BULLS AND COWS OF THE GREY SEAL, *HALICHOERUS GRYPUS* FAB.

BY

H. R. HEWER

Department of Zoology, Imperial College, London

AND

K. M. BACKHOUSE

Department of Anatomy, Charing Cross Hospital Medical School, London

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(With 5 plates)

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INTRODUCTION

It is generally stated (Davies, 1949, Wynne-Edwards, 1954, Hewer, 1957) that the bull grey seal has a convex profile while the cow has a straight one. (Pl. 1, figs. 2a and 4a). This distinction has the advantage that it can be applied to the part of the body most frequently seen when seals are in the water. There are, however, several disadvantages. The first is almost one of principle ; that a character observable from only one angle of view greatly restricts its applicability. Thus when seals are hauled out a great proportion lie on their sides and the head profile is invisible. Further, seals in the sea but viewed from a cliff, rarely present a recognisable profile. A second disadvantage is that bulls only gradually develop the convexity in the naso-frontal region. Consequently young bulls may show a profile which is hardly distinguishable from that of a mature cow. Conversely very old cows gradually obtain a slight convexity of profile and thus simulate the condition seen in bulls.

There are several other recognised sexual differences ; bulls have a greater breadth of the muzzle, a thicker neck and generally a more heavily built body than cows. All of these differences are comparative and are less obvious in younger bulls than in the relatively few bulls which are normally found holding territory on the breeding grounds. Only in a breeding colony of grey seals are these characters satisfactory for sexing animals. Even here, on occasion, as one of us has shown (Hewer, 1957) the presence of many less mature bulls may raise considerable problems of sex identification. When young bulls are included in haulouts of both sexes, separation of bulls and cows is very difficult as we have found, in Pembrokeshire, on the Farne Islands, and in the Hebrides.

CRITERION FOR THE IDENTIFICATION OF BULLS AND COWS

For the past four years the authors have been studying the behaviour of the grey seal in the non-breeding part of the year, and a definite means of distinguishing between bulls and cows became absolutely necessary if any accurate data were to be obtained. Careful examination of all material available to us, both preserved and living, has brought to light a character which seems to meet all the necessary requirements.

This character may be briefly stated as follows :—

In the grey seal, apart from the generally darker overall tone of the back, which shades into a lighter belly (more noticeable in cows than in bulls), there are two tones contributing to the colour pattern—a darker and a lighter.

In bulls *the darker tone* is the more extensive, being *a continuous background* with lighter patches. This description is applicable whether the colour involved be brown, black, dark grey or mid-grey as the *darker* tone, the lighter tone being a lighter shade of the same colour, even to white or, in some bulls, tinged with yellow or tawny. In the limiting form, the animal may appear entirely dark. (Pl. 1, figs. 1, 1 a, 2 and 2a).

In cows the darker tone is restricted to separate and discrete spots or patches (sometimes quite extensive) but *the lighter tone is the continuous one*. The limiting form here may be one with no darker spots at all in the back and only a few on the belly. Much the same range of colours is found in cows as in bulls. (Pl. 1, figs. 3, 4 and 4a).

This criterion has a number of advantages :—1. It is based on *tone* and therefore eliminates colour differences between individuals. 2. It is based on the *differences in tonal distribution* in one and the same animal and so eliminates the overall changes in colour and tone due to the annual moult. 3. It can be applied to *almost any part of the body* ; even a single fore-flipper will show the difference in most seals. 4. It can also be observed in either *wet or dry seals*, provided they have not rolled in sand. 5. It can be seen from *any angle*, provided the only part visible is not both wet and reflecting the sun directly. 6. It is applicable to all ages with the possible exception of the obviously juvenile (which are often erroneously referred to as "yearlings").

Reference to the illustrations on Pls. 1–5 will show this critical feature and the conditions under which it can be observed.

This character was originally noticed in the field when the authors had a large number of seals (up to 180) under continuous observation, and has since been checked in a number of ways. First, in the field, identification was verified by observation of the penial aperture in the bull or its absence in the cow. In the breeding season, on the breeding beaches, confirmatory sexual behaviour has been considered sufficient, but at other times of the year this may not be used as many younger bulls show behaviour similar to that of cows. (Backhouse & Hewer, 1958). These observations on live seals have covered several hundreds of individuals. Secondly it has been checked on the available skins in the British Museum (Natural History) and on eleven pieces of skin from three bulls and eight cows from Berwick-on-Tweed. These pieces of skin were removed from the centre of the back (Pl. 2, figs. 8 and 9). Thirdly all available photographs of grey seals whose sex is known otherwise have been examined. Fourthly the three grey seals (one bull and two cows) in the Gardens of the Zoological Society of London have also been seen. (Pl. 5, figs. 17 and 18).

In all instances, save one, the character clearly held good. The single exception was a cow seen this autumn whose dark spots were so numerous that we were doubtful about the sex until she was seen to be the mother of a pup. The dark patches were confluent sufficiently extensively to give the impression that the dark tone was the continuous one. Mr J. M. Davies (now in Tasmania) informs us (in. litt.) that he has a water colour drawing of a cow seal on Ramsey Island which was apparently equally dark toned. These then represent the only possible exceptions observed, and are therefore less than 1 per cent of all bulls and cows examined.

Juveniles (less than 4 feet 6 inches in total length) have not yet been sufficiently studied, since they are comparatively rarely seen. It should be noted however that the pieces of pelt shown in Pl. 2, figs. 8 and 9 are from fairly young animals which would be classed as juveniles if seen on the breeding grounds. In these the sexual differences are quite distinct. The male characteristics were also quite clear on " Sid " in the London Zoo when two-and-a-half years old, at which age he was first observed for this feature. The female characteristics were also quite clear in the two London Zoo cows as moulters on arrival.

It is possible that all moulters do not show the difference with the same distinctness. Insufficient animals have been observed so far to enable a definite statement to be made, but the tonal character held good in all those moulters examined.

APPLICATION OF CRITERION TO VARIOUS PARTS OF THE BODY

The Head and Neck. These parts are exposed most frequently when the seal has surfaced and is " looking round " (Pl. 2, fig. 6), or is floating vertically asleep in the attitude to which we have given the term " bottling " (from its resemblance to a floating bottle, Pl. 2, fig. 7). The top of the head and face should be neglected being usually monotone, but the throat and sides of the neck display the distinctive character excellently (Pl. 1, figs. 1a, 2a and 4a; Pl. 2, figs. 6 and 7).

The Back. This may be the only part seen if the seal is floating horizontally but it shows the distinctive character quite clearly (Pl. 2, fig. 5).

The Belly. In the bull the tonal values are quite distinctive but in the cow the anterior part on the thorax towards the throat is always the best. However the majority of cows display the character all over the belly. It is particularly noticeable in cows because the ventral lighter tone is itself much lighter than the dorsal lighter tone whereas the darker tones are usually similar, making the contrast in tones greater than on the back.

The Flippers. The fore flippers display it well but the hind flippers are not usually reliable since they are folded in repose on the land, thus obscuring the tonal pattern, and are invisible in the ripples of the water.

Thus only the top of the head, muzzle and hind flippers cannot be used for this criterion.

In the past it has been frequently stated (Darling, 1939 & 1947, Davies, 1949, Matthews, 1952) that the bulls are generally darker than the cows, but exceptions have always been made, together with references to colour

variations. It is now clear that this generally darker appearance of bulls is due to the continuous dark tone and that even the "exceptions" fall into line when the *relative* tones in the same animal are taken into account.

The authors had become aware of their own growing doubts on the identification of bulls and cows of all ages by previously accepted criteria and hence extra care was taken in recent years. Fortunately no figures have been published by them which are subject to revision and criticism since the problem only assumed serious proportions when dealing with non-breeding populations. The numerical data published by one of them (Hewer, 1957) were sufficiently approximate to permit a variation of about (± 5 per cent) without affecting the conclusions. Moreover the author was already conscious of the difficulty and is of the opinion that any error made by him did not exceed that percentage.

They feel justified, from their own experiences, in viewing with gravest suspicion any *confident* statement relating to the proportions of bulls and cows based upon any criteria other than that now described, unless the external genitalia of the seals were observed.

ACKNOWLEDGMENTS

The pieces of pelt shown in Pl. 2, figs. 8 and 9, with several others, not illustrated, were kindly sent by Dr J. Lockie of Nature Conservancy, from specimens killed in the Berwick-on-Tweed area. He also sent the corresponding measurements and material which has permitted an accurate age to be given for them.

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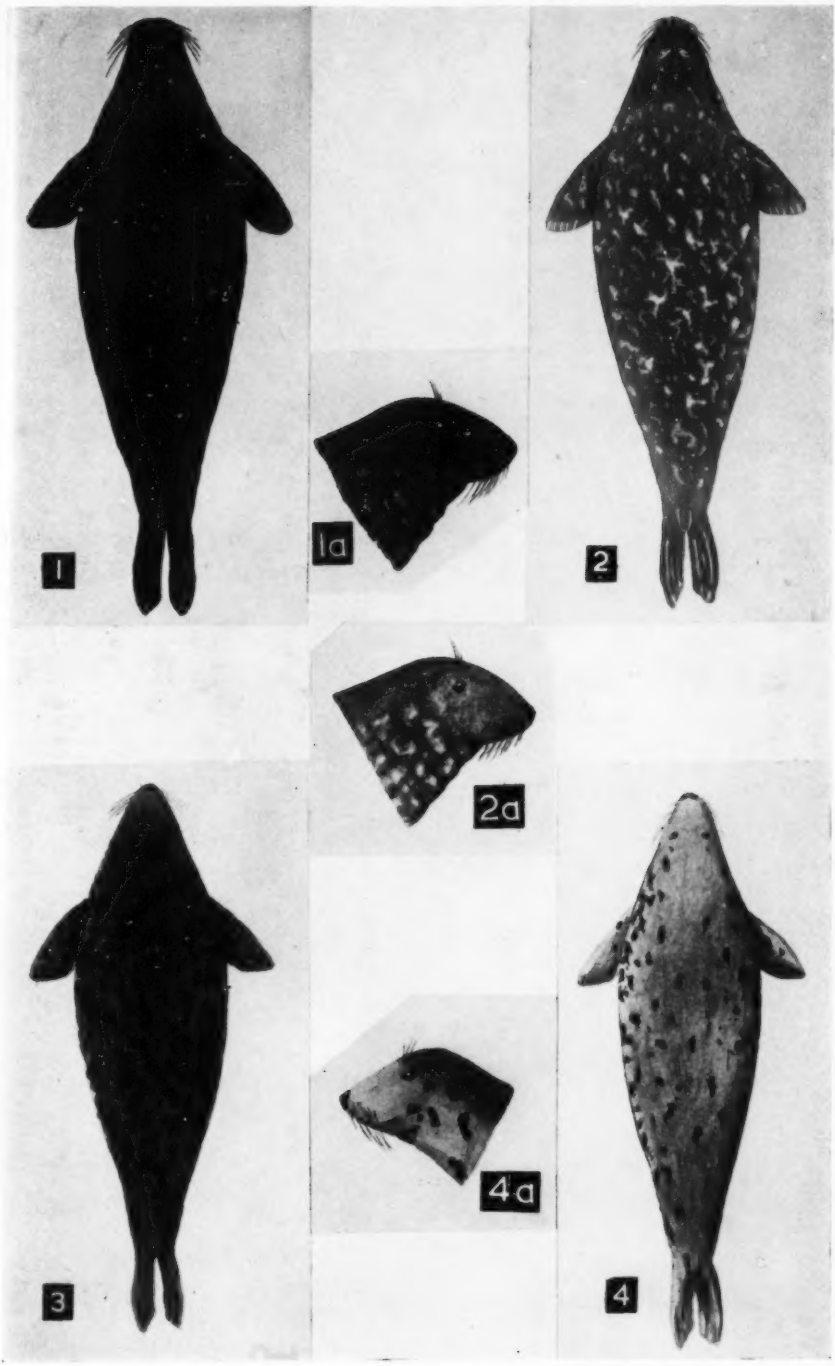
EXPLANATION OF PLATES

Plate 1

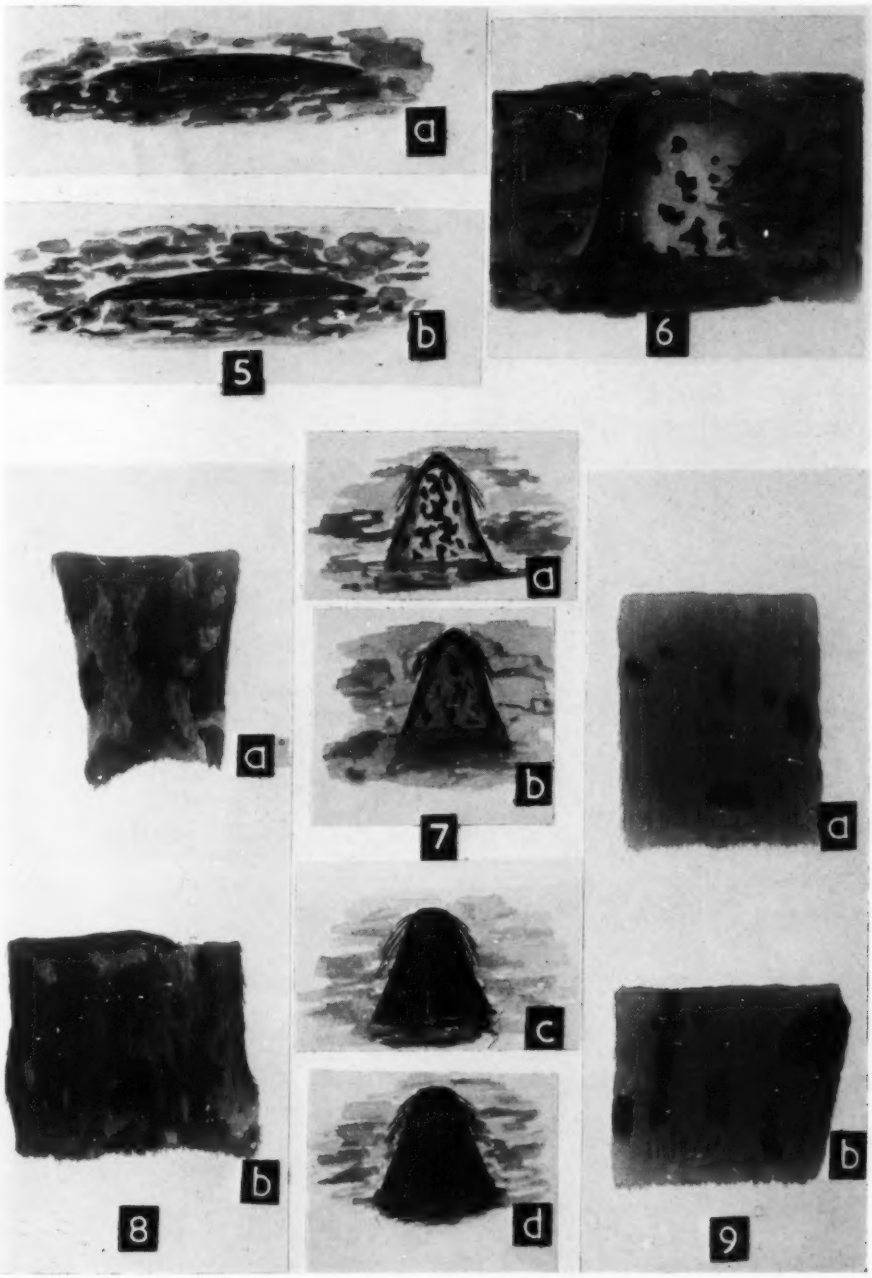
Fig. 1.—Mature bull of dark type. 1a, Head of same.
„ 2.—Mature bull of light type. 2a, Head of same.
„ 3.—Mature cow of dark type.
„ 4.—Mature cow of light type. 4a, Head of same. (All from water-colour sketches).

Plate 2

Fig. 5.—Backs of bull (a) and of cow (b) as seen when floating.
„ 6.—Side view of head of cow in typical "treading water" posture.
„ 7.—Ventral views of seals' heads as seen when "bottling"; a and b, cows; c and d, bulls.
„ 8.—Pieces of pelt from the centre of the back of two bulls; a, 1½ years, overall length 70 ins.; b, 1½ years, overall length 67 ins.
„ 9.—Pieces of pelt from the centre of the back of two cows; a, ¾ year, overall length 57 ins.; b, ¾ year, overall length 60 ins. (All from water-colour sketches).



Field identification of bulls and cows of the Grey Seal.



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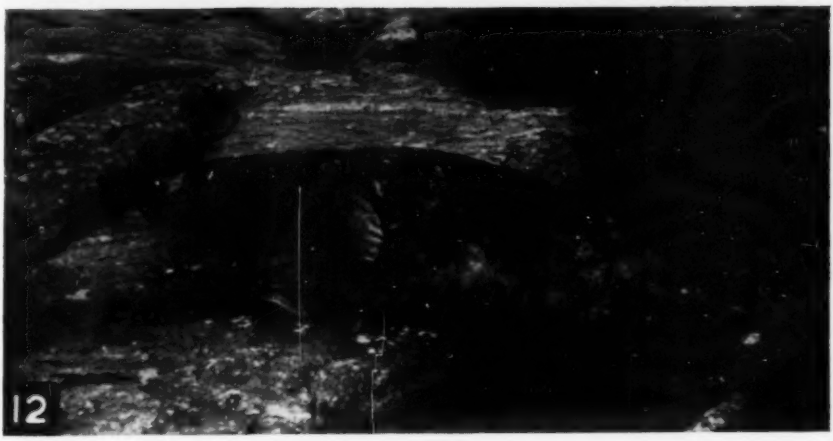

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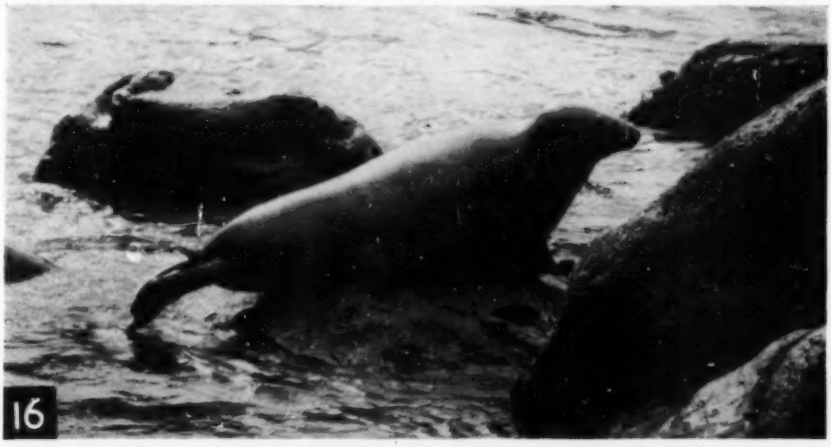

Field identification of bulls and cows of the Grey Seal.

PLATE 3

Fig. 10.—Mature bull, holding territory, on Brownsman Is., Farne Islands, Northumberland. Wet pelt.

„ 11.—Mature bull, holding territory, on Shillay, Outer Hebrides. Dry back, wet lower sides.

„ 12.—Mature bull, not holding territory, on Shillay, Outer Hebrides. Dry pelt.

(All from untouched photographs. Figs. 11 and 12 from photographs by Mr J. W. Siddorn).

PLATE 4

Fig. 13.—Breeding cow, Ramsey Is., Pembrokeshire. Wet pelt. A dark type with confluent dark spots on chest ; but note back and sides.

„ 14.—Breeding cow, Ramsey Is., Pembrokeshire. Dry pelt. Light type.

„ 15.—Breeding cow, Brownsman Is., Farne Islands, Northumberland. Wet pelt. A typical example ; note character clearly shown on wet fore-flipper. (All from untouched photographs).

PLATE 5

Fig. 16.—Breeding cow, Ramsey Is., Pembrokeshire. Wet pelt with light shining towards observer. Note that the character is clear even under these conditions.

„ 17.—Cow, 5½ years old, from Farne Islands, in London Zoo. Wet pelt. Another dark type.

„ 18.—Bull (" Sid "), 7½ years old, from Devon in London Zoo. Wet pelt. (All from untouched photographs).

SPHAERONELLA SEROLIS MONOD, AND A NEW SPECIES OF *RHIZORHINA*, COPEPODS PARASITIC ON THE ISOPOD *SEROLIS BROMLEYANA* SUHM (CRUSTACEA)

BY

J. GREEN

Bedford College, University of London

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(With 16 figures in the text)

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INTRODUCTION

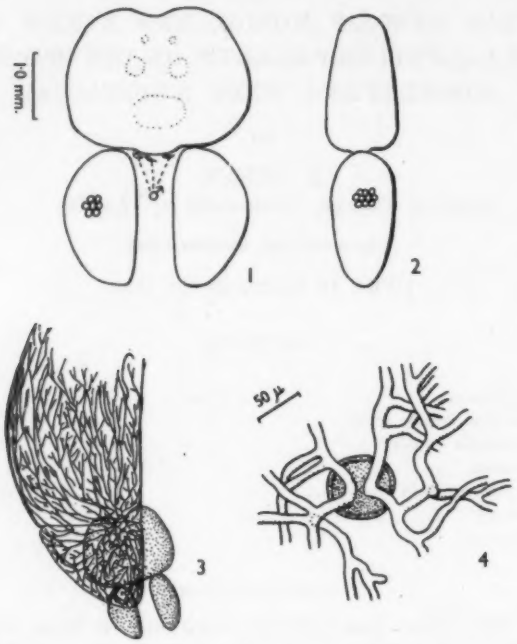
The genus *Rhizorhina* has hitherto been known from a single species, *R. ampeliscae* Hansen (1892), which was originally described from Denmark and Norway, and had not been recorded elsewhere until recorded by Green (1958) from Guernsey and the Clyde. The genus is remarkable because it is parasitic on Crustacea, while all the other members of the family to which it appears to belong, the Herpyllobiidae, are parasites on polynoid polychaetes. *Rhizorhina ampeliscae* is a parasite of members of the amphipod genus *Ampelisca* ; the new species described here parasitises an isopod, and was collected by the New Zealand Expedition to Chatham Island.

Family HERPYLLOBIIDAE

RHIZORHINA SEROLIS, sp. n.

Description of the female. The body is bean shaped (Figs. 1 and 2), about 2·0 mm. long, 2·5 mm. wide, and 1·1 mm. thick. The dotted areas in Fig. 1 indicate slight depressions of the surface. There are no appendages. A small sclerotised ring is present around the mouth, from which issue two pairs of root-like processes. These roots, which are 10–14μ in diameter, pass into one of the pleopods of the host and ramify greatly (Fig. 3). The egg sacs are variable in size, but when fully developed they are pear shaped, about 1·95 mm. long and 1·20 mm. at the greatest width. Each egg has a diameter of about 0·13 mm. The males attach to the females, at the posterior end between the egg sacs.

Description of the male. The male is very similar to the male of *R. ampeliscae.* The body (Fig. 5) is of a typical copepod shape, but there are



Figs. 1–4.—*Rhizorhina serolis*. 1, female, dorsal view. 2, female, lateral view. 3, pleopod of *Serolis bromleyana* with female attached, showing the extent of the rooting system from the mouth. 4, detail of the rooting system near the mouth.

only two pairs of swimming legs. The size is only a small fraction of that of the female ; the total length, excluding setae, is about 0·2 mm.

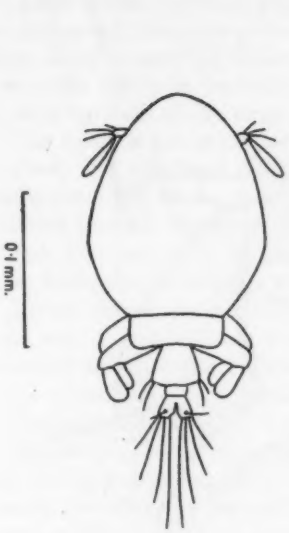
Each antennule has three podomeres, the first with two setae, the second without setae, and the third with nine setae and a large flattened aesthetasc which is practically as large as the podomere. This aesthetasc is inserted sub-terminally and its long axis is usually inclined at an angle to the long axis of the third antennulary podomere.

The antennae are reduced to small projections near the bases of the antennules.

The mandibles are thin and stylet shaped, projecting slightly through a small sclerotised ring which indicates the position of the mouth.

The maxillules are each represented by two small forwardly projecting processes which lie between the bases of the antennules. Hansen interprets these structures in *R. ampeliscae* as maxillae, but by comparison with the larvae of the Choniostomatidae it is clear that the same sequence of appendages can be made out and that the maxillae are the larger appendages placed more posteriorly.

The maxillae have a large basal podomere and a much narrower terminal podomere which bears a long stout spine and a slender seta.



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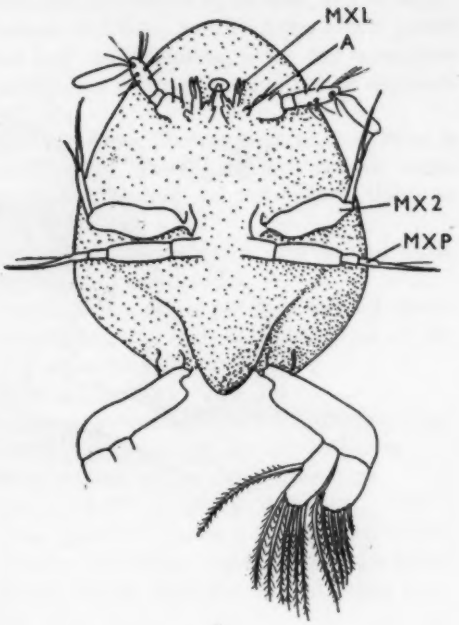

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Figs. 5–6.—*Rhizorhina serolis*. 5, male, dorsal view, the setae on the swimming legs have been omitted. 6, thorax and head of male, ventral view. A—antenna ; MXL—maxillule ; MX2—maxilla ; MXP—maxilliped.

The maxillipeds each have three podomeres, the last bearing a strong spine and a slender seta.

The two pairs of swimming legs are similar in structure. The endopods bear seven plumose setae, one of which is inserted on the inner border, and the exopods bear six setae which decrease in length towards the outer margin.

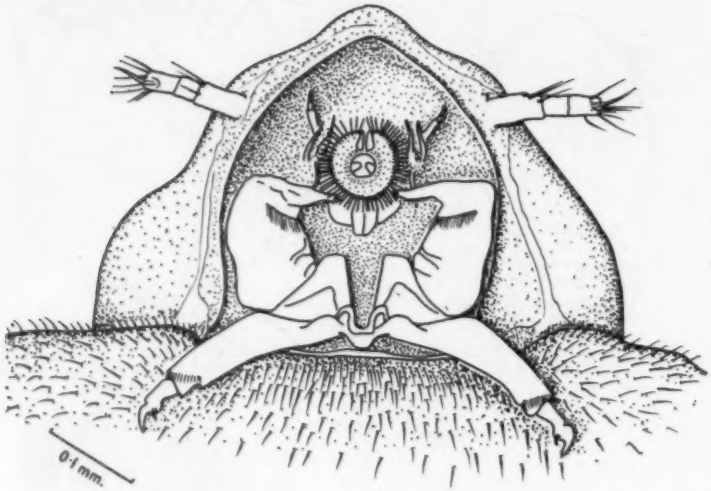
The caudal rami bear four terminal setae, of which the median ones are the longest. There is also a small seta on the dorsal surface of each ramus.

Occurrence. This species was numerous on the pleopods of *Serolis bromleyana* Suhm. As a rule only one female was attached to each host. The hosts were collected by the New Zealand Chatham Island Expedition from a depth of 403 metres on Chatham Rise (Station 6, 43° 40′ S., 179° 28′ E.).

Family Choniostomatidae

Sphaeronella serolis Monod

This species was described by Monod (1930), but owing to the limitations of his material certain details of anatomy were not described. The material described in the present paper was obtained from a single female of *Serolis bromleyana*, which was also infected with *Rhizorhina serolis*. The brood pouch of the isopod contained four large females of *Sphaeronella*, one small female,



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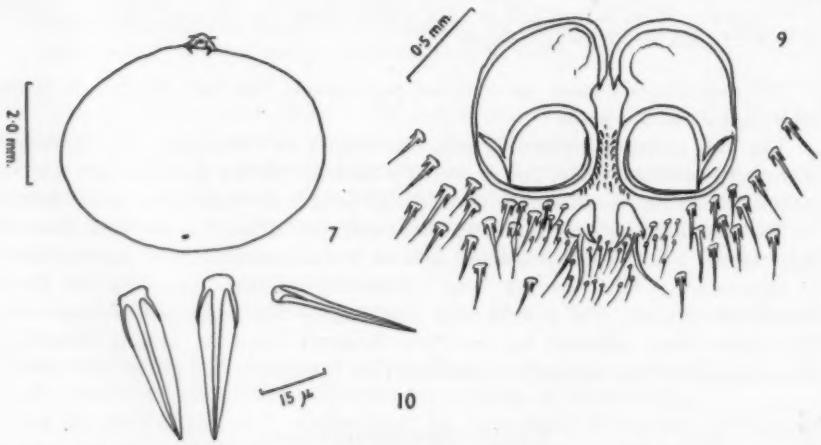

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Figs. 7–10.—*Sphaeronella serolis*. 7, adult female, ventral view. 8, head of adult female, ventral view. 9, genital area of adult female. 10, setae from near the genital area of an adult female.

two adult males, one male pupa with a cast larval skin by its side, and seventy-two egg sacs ! Assuming that no females had been lost from the brood pouch (there is no reason for believing that any were missing, since the oostegites were quite firmly in position) this implies an average production of eighteen egg sacs by each of the large females.

The females are much larger than any other choniostomatid, but have a relatively minute head. My examination of the appendages reveals some differences from those described by Monod, but I do not regard them as sufficient grounds for establishing a new species.

The first podomere of the antennule bears three setae, the second lacks setae, while the third bears seven setae and an aesthetasc.

Monod shows the maxillules as having but a single process, but my specimens were found to have three processes forming each maxillule, one of the processes was directed backwards, the other two forwards.

No appendages were found on the trunk.

The genital areas (Fig. 9) on my specimens were much better developed than on Monod's. The caudal rami lie immediately behind the genital area and bear two long setae as well as a stout inner spine and a small outer spine. The setae at the sides and behind the genital area are peculiar in structure. When viewed with a 1/6th inch objective they appear to have a long central prong and two small outer prongs, but critical observation using an oil immersion objective shows that the outer prongs are united with the central prong by a very thin membranous structure (Fig. 10).

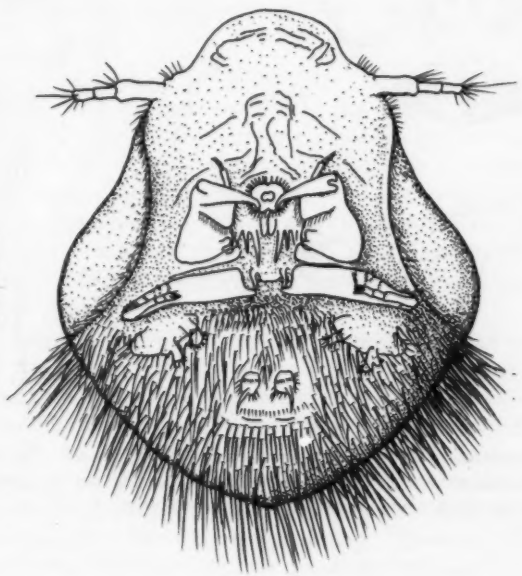
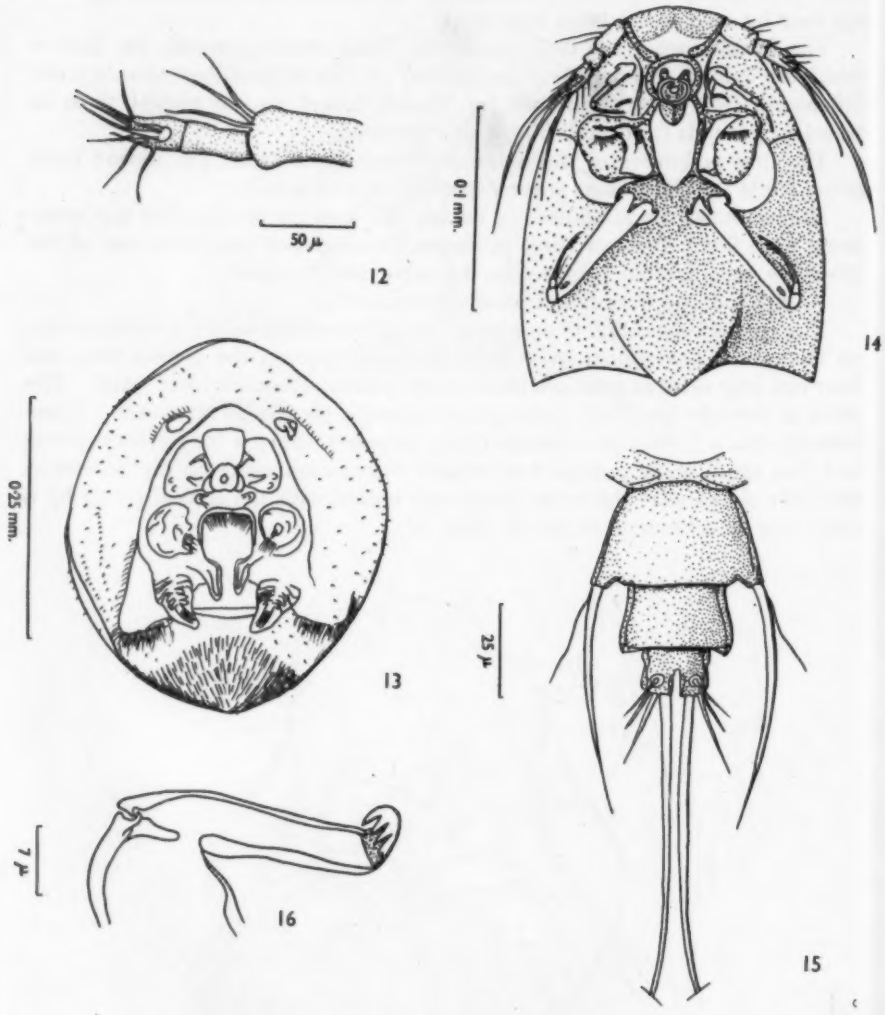


Fig. 11.—*Sphaeronella serolis*, adult male, ventral view.



Figs. 12–16.—*Sphaeronella serolis*. 12, left antenna of adult male. 13, pupal male, ventral view. 14, larva, ventral view of thorax and head. 15, larva, dorsal view of abdomen. 16, larva, terminal podomere of maxilla, ventral view.

The male (Fig. 11) is much smaller than the female, only reaching a length of 0·65 mm. The frontal border projects in front of the antennules, forming a flat, roughly semicircular, structure in front of the globular body.

The structure of the trunk limbs is very difficult to see because the hind part of the trunk is so densely covered with setae.

The maxillules of the male could not be found.

The male pupa is shown in Fig. 13 ; the total length was 0·40 mm. The pupal skin bore a few setae which were irregularly distributed.

A cast off larval skin was found attached to the pupa. This was 288μ long, excluding the long setae on the caudal rami, which added a further 169μ to the length.

The larval appendages are of the usual choniostomatid pattern. The terminal podomere of the antennule bears ten setae, two of which are long and terminal, and a very long aesthetasc. The antennae are well developed, of three podomeres, the last bearing a long plumose setae. The maxilla shows an unusual modification of the tip, which is bent downwards and produced to form three strong teeth (Fig. 16).

The first abdominal segment bears a large spiniform seta and a much finer shorter seta on each side. The caudal rami each bear a very long median seta, two shorter outer setae and a small dorsal seta (Fig. 15).

Occurrence. This species was described by Monod (1930) from the brood pouch of *Serolis pagenstecheri* Pfeffer, from Westcumberland Bay, South Georgia. It is now recorded from the brood pouch of *Serolis bromleyana* Suhm from a depth of 403 metres on Chatham Rise.

DISCUSSION

One striking feature of these records is the erratic occurrence of these species in Nature. As far as I am aware, *Sphaeronella serolis* has not been recorded since Monod's original description ; and now it is found on another species of *Serolis* from a locality about five thousand miles from the original one. It might be thought that this is a widespread species that has been overlooked, but I have searched through the large collection of *Serolis* species in the British Museum (Natural History), and have not found any specimens of *Sphaeronella* or of *Rhizorhina*.

A point of general interest is the great resemblance between the male of *Rhizorhina* and the larva of *Sphaeronella* ; indeed the male of *Rhizorhina*, if found alone, could easily be mistaken for a larval *Sphaeronella*, except when it has spermatophores formed within the body. There are differences in the appendages, as can be seen when Figs. 6 and 14 are compared. But the overall resemblance is so great that one reaches the conclusion that the male of *Rhizorhina* is neotenic, and that the Herpyllobiidae have advanced further in their modification than the Choniostomatidae. This is borne out by the females ; in the Herpyllobiidae they are generally without any appendages at all, while the choniostomatids have well developed head appendages and often have diminutive trunk appendages as well.

ACKNOWLEDGMENTS

I am grateful to Dr R. B. Pike and Dr J. P. Harding for the opportunity to examine these specimens, also to Dr Harding for reading and criticising the manuscript.

SUMMARY

The male and female of *Rhizorhina serolis* sp. n. are described and figured. This copepod is parasitic on the isopod *Serolis bromleyana*, from Chatham Rise, between Chatham Island and New Zealand.

Sphaeronella serolis Monod is recorded from the same host and locality. The hitherto unknown larva and male pupa of *S. serolis* are figured.

The male of *Rhizorhina* shows a great similarity to the larva of *Sphaeronella*, and is considered to be neotenic.

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PNEUMATIC OSTEOLYSIS IN THE ELEPHANT SKULL

BY

A. J. E. CAVE, M.D., D.Sc., F.Z.S.

St. Bartholomew's Hospital Medical College, University of London

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(With 6 figures in the text)

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INTRODUCTION

In their classic monograph on Sivalik palaeontology Falconer & Cautley (1847) depicted, in norma frontalis, two skulls of different races of the modern Asiatic elephant, which they designated respectively *E. indicus* var. *dauntela* and *E. indicus* var. *mukna*. (Their figure is herein reproduced as Fig. 1). The drawing of the *E. indicus* var. *dauntela* skull displays two obtrusive and curious "ossicles" or "patches" of oval, sutural, outline, each situate in the deeply concave incisive fossa of the corresponding moiety of the skull. These "ossicles", unlettered in the original figure, are nowhere referred to in the accompanying text. Their bilateral disposition and symmetrical outline preclude any pathological origin, their remoteness from the interpremaxillary suture obviates interpretation of their presence on grounds of "Wormian bone" formation, and clearly they cannot constitute adventitious cranial elements.

The Falconer-Cautley figure was reproduced by Osborn (1942) in his monograph on the Proboscidea, but without any reference to these premaxillary "ossicles" or "patches". Grassé (1955) likewise reproduced the ancient figure and was equally silent as to the presence of these curious " ossicles ". Somewhat surprisingly no figure is given, or mention made, of them in any other of the numerous published accounts of the osteology or cranial anatomy of the elephant.

Yet examination of the extensive series of elephant crania in the collections of the British Museum (Natural History) reveals such a condition of parts to be of common, if not invariable, occurrence in fully mature or old specimens of both the Asiatic and the African species : and very little investigation is required to establish the true nature and significance of these premaxillary pseudo-ossicles.

OCCURRENCE OF INFRANARIAL PSEUDO-OSSICLES

Of twenty-six crania of *Elephas maximus* Linn. examined (representing all ages from birth to senescence) the pseudo-ossicles were observable in six specimens (i.e. in 23 per cent of all skulls), their occurrence being confined to the eighteen unmistakably adult members of the series (wherein their incidence was 33·3 per cent).

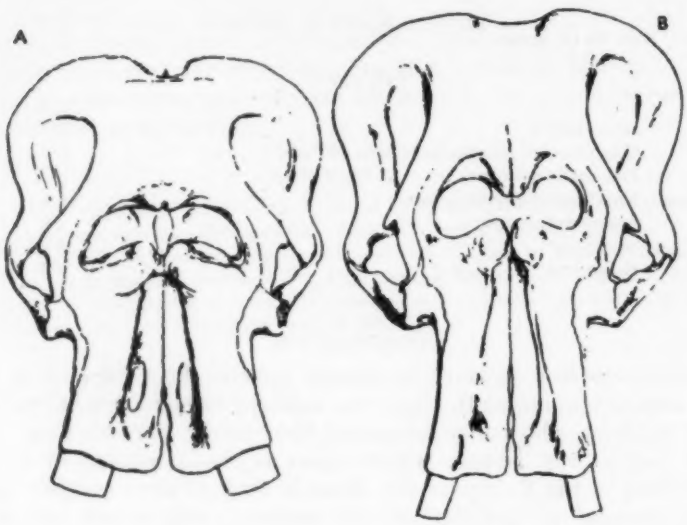

Fig. 1.—Skulls of (A) *Elephas indicus* var. *dauntela*; (B) *Elephas indicus* var. *mukna*, from Falconer and Cautley (1847). The *dauntela* figure shows a pair of oval, infranarial "ossicles".

Of fifty-three crania of *Loxodonta africana* Blumenbach examined (ranging from infancy to advanced age) the pseudo-ossicles were observable in twelve specimens (i.e. in 22·6 per cent of all skulls), their occurrence being confined to the twenty fully adult members of the series (an incidence therein of 60 per cent).

As will be shown, the greater frequency of "ossicle" occurrence in adult African elephant skulls is to be correlated with the relatively greater size and weight of the tusks in this species, which necessitate a relatively larger and heavier cranium for both their support and their functional employment. Data given by Dollman & Burlace (1935) regarding "record" tusks in the two elephant species clearly illustrate the considerably greater tusk-size and tusk-weight attained by the African elephant when contrasted with the Asiatic animal of comparable age.

(Recorded maximal tusk length in the Asiatic elephant is less than, in the African elephant more than, 10 feet. The maximal recorded individual tusk weight for the Asiatic species is 161 lb., but for the African species as much as 293 lb.).

PNEUMATIC OSTEOLYSIS

Thus the adult African elephant skull carries a relatively greater weight and bulk of ivory, a burden necessitating a relatively greater skull-mass, with increase of both the tusk-bearing maxillary component and the occipital component giving attachment to the supportive nuchal musculature. The potential mechanical disability of any increase in bulk of nuchal musculature (to maintain the additional cranial load) is obviated by a compensatory lightening of the load itself, without detriment to its mechanically necessary bulk. This lightening is effected, conveniently and efficiently, by a relatively more extensive and more persistent pneumatisation of most of the component cranial elements.

In such pneumatisation an important rôle is played by the paranasal sinuses. Expectedly, therefore, and as dissection reveals, paranasal sinus elaboration in the African elephant skull surpasses in extent that obtaining in the Asiatic elephant skull.

The elephant skull undergoes pneumatisation to an extraordinary, possibly unique, degree, an anatomical character which has received notice in all general works on elephant morphology. The functional significance of this pneumatisation (the achievement of lightness in a cranium inevitably rendered huge by considerations of tusk-bearing and muscle attachment) was correctly assessed by such early writers as (Moulin, 1682; Blair, 1710; Perrault, 1734; Camper, 1802) as well as by such later authorities as Owen (1866) and Flower (1885). Flower improved on previous accounts by enumerating the cranial bones pneumatised (which include vomer and mesethmoid) and his enumeration is retained in recent works (e.g. Weber, 1928).

Details as to the number, situation and extent of the sinuses themselves are available, however, only in a fairly recent specialist literature (Paulli, 1900; Anthony & Coupin, 1925; Boas & Paulli, 1925). In this literature, concerned largely with the examination of young, immature and youngish adult specimens, anatomical details are wanting touching the precise extent and manner of pneumatisation of the maxilla and premaxilla in fully mature or old specimens. Flower & Lydekker (1891) indicated, however, that wherever two originally distinct cranial elements establish contact pneumatisation may extend from the one into the other; also that in old animals almost all the sutures undergo obliteration.

Anthony & Coupin (1925) recognised four paranasal sinuses, viz. sphenoidal, maxillary, premaxillary and naso-fronto-parietal. They stressed the precocious development of the premaxillary, in relation to the maxillary, sinus in both species of elephant, a precocity correlated with the proportionate growth rates of premaxilla and maxilla.

Boas & Paulli (1925) recognised sphenoidal, nasal and maxillary sinuses, as well as a superior and an inferior premaxillary sinus. Their superior premaxillary sinus is but the ascending portion of the maxillary sinus proper; the inferior premaxillary sinus (premaxillary of Anthony & Coupin) may be a separate entity with a discrete ostium or it may be replaced entirely by the maxillary sinus.

Although no detailed information is seemingly available concerning the

precise topography and mutual relationships of the premaxillary and maxillary sinuses in the maximally-pneumatised fully adult cranium, it would appear fairly obvious that the maxillary sinus is the dominant pneumatising cavity in the subnasal component of the facial skeleton, a concept receiving support from certain of the magnificent plates (Pls. 26, 28, 29, 31) of Boas & Paulli (1925).

MAXILLARY SINUS ENLARGEMENT

The maxillary sinus is certainly the agent responsible for the appearance of the pseudo-ossicles to be encountered in the premaxillary region of so large a proportion of fully adult elephant skulls, and there can be no doubt that it undergoes a steadily progressive enlargement throughout life *pari passu* with the steady increment of tusk-size and -weight, and the consequent necessity for a compensatory pneumatic lightening of the cranium.

The elephant tusk (incisor) is socketed within the premaxilla, whose infranarial portion, between the tusk alveolus and the median plane, forms the concave floor of the incisive fossa, and is supported by the underlying palatine process of the maxilla. In young and immature skulls, the incisive fossa is shallow : with advancing age, and corresponding increase in size and weight of the tusk, the alveolar boundary of the fossa becomes increasingly prominent and the fossa itself correspondingly deeper. Mature or old animals (i.e. specimens showing the last molar in use) manifest the greatest depth of incisive fossa and in a large proportion of such specimens a pseudo-ossicle is present in the fossa floor.

In Fig. 2 is depicted the infranarial region of an oldish African elephant (B.M. 1925.5.18.1) with characteristically deep incisive fossae. In the left fossa the premaxilla displays a small compact cluster of perforations, each of which represents a limited absorption of the bone. In the right fossa a similar cluster has become confluent by disappearance of bone between the several fenestrae and now forms a premaxillary deficiency of appreciable size through which the underlying maxilla is visible. A crack, simulating a suture, is also apparent, leading infero-laterally from the upper end of the inter-premaxillary suture and medial thereto the premaxilla is considerably thinned. The changes illustrated ("suture" formation, premaxillary thinning and punctate premaxillary atrophy) represent the initial stage of maxillary sinus osteolysis.

In Fig. 3 are shown the infranarial regions of (a) an Asiatic elephant (B.M.1936.6.26.1) and (b) an African elephant (BM.28.11.13.1), both fully adult. Each of the four incisive fossae manifests a curious "patch" or pseudo-ossicle, circumscribed by an oval continuous "suture", from which a minor "suture" may start. Exploration by seeker beneath the serrated edge of the circumscribing "suture" establishes clearly that within the "suture" the premaxilla has disappeared and that the bone forming the floor of the intra-sutural area (i.e. the " ossicle " itself) is simply the exposed superficial aspect of the underlying maxilla. This second stage, that of the fully-formed oval "ossicle" of "sutural" outline, is that most frequently encountered in oldish adult elephant skulls, both Asiatic and African. (The premaxillary bone remaining, i.e. that outside the " ossicle ", adheres closely to the maxilla at

the circumscribing " suture " and hence not in every specimen is it possible, without damage, to introduce a suitable seeker underneath the " suture ").

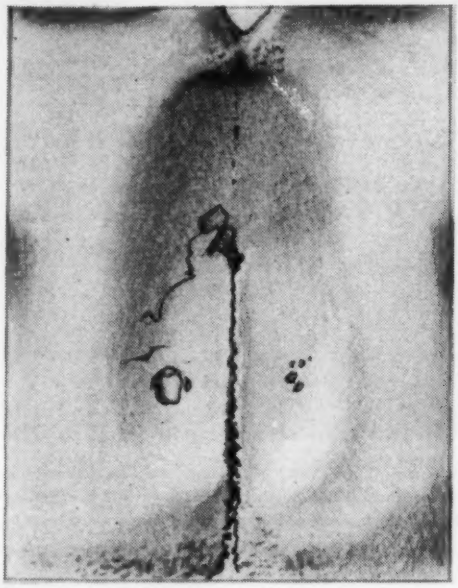

Fig. 2.—*Loxodonta africana* (B.M.1925.5.18.1). Infranarial region showing initial formation of incisive fossa "ossicle", viz. punctate absorption of premaxilla and commencing circumscribing "suture".

In Fig. 4 the infranarial region is portrayed of (a) an Asiatic elephant (B.M.1948.4.29.2) and (b) an African elephant (B.M.1947.2.27.7), both older animals than those represented in the previous text-figures. Both specimens confirm the interpretation of the bone-changes advanced in connexion with the previous two specimens ; for in each of the present specimens (on the left side in the Asiatic skull, on the right side in the African skull) the strip of premaxilla normally remaining between the "ossicle" and the midline is accidentally broken way and the continuity of the underlying maxilla up to the intermaxillary suture is plainly established.

These two skulls manifest a further (third) stage in maxillary sinus osteolysis. The floor of the "ossicle" (i.e. the maxillary bone itself) is now yielding to sinus pressure and displays a number of discrete perforations of roundish or irregular outline. A probe introduced through any one of these leads directly into the maxillary sinus. With continued life of the animal, the "ossicular" area of the maxilla becomes increasingly perforate, until, in advanced age, the condition of parts represented by Fig. 5 is attained. This figure shows the infranarial region of an obviously old African elephant (B.M.49.532). In each incisive fossa not only is the "ossicular" maxillary bone multiply perforate but the whole floor of the infranarial fossa is cribriform

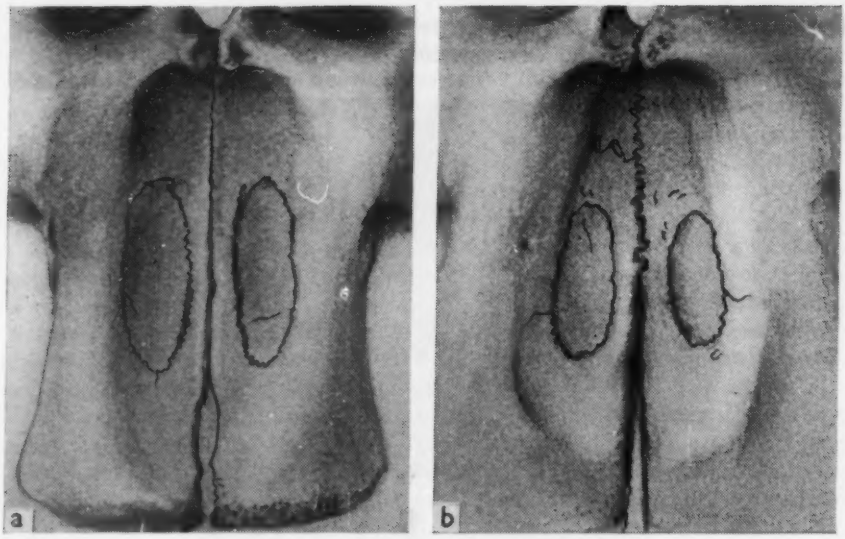

Fig. 3.—a=*Elephas maximus* (B.M.1936.6.26.1) and b=*Loxodonta africana* (B.M.28.11.13.1). Infranarial regions showing established "ossicles" in the incisive fossae floors. The exposed bone within the circumscribing "suture" is the maxilla.

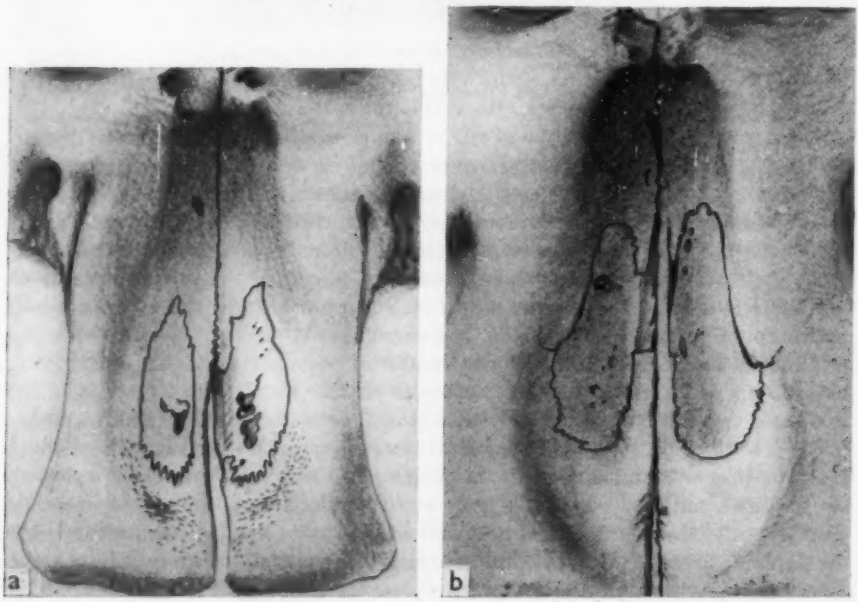

Fig. 4.—a=*Elephas maximus* (B.M.1948.4.29.2) and b=*Loxodonta africana* (B.M.1947.2.27.7). Infranarial regions with established "ossicles". The (maxillary) bone of each "ossicle" shows commencing pneumatic osteolysis.

from osteolysis. Perforations, representing islands of bone absorption, are abundant between the "ossicular" maxillary area and the summit of the infranarial region : in this upper incisive region each perforation involves the thinned overlying premaxilla plus the thinned underlying maxilla and an introduced probe enters the maxillary sinus directly. This conversion of the floor of the quadrate infranarial fossa from a smooth bony sheet into a cribriform lacework is the ultimate—and sufficiently dramatic—phase attained by maxillary sinus osteolysis. Since its development necessitates great longevity it is the least common manifestation of maxillary sinus osteolysis, and was encountered but once in the material studied.

(The perforations present in the macerated skull are, in life, completely closed by the apposition of the external periosteum and the maxillary sinus mucoperiosteum ; this composite membrane alone intervenes between the cavity of the maxillary sinus and the superficial infranarial soft tissues).

The series of elephant crania just described establishes unequivocally the genesis and true nature of the curious "ossicle" known for so long to occur in the floor of the incisive fossa. The entire surface of that "ossicle" is nothing other than the aboral aspect of the palatine process of the maxilla, exposed by osteolytic removal of part of the overlying premaxilla, a removal effected by the continuously expanding maxillary sinus. The successive stages are clearly demonstrable whereby this sinus, in its sustained effort at cranium-lightening, presses the relevant portion of the maxilla with increasing and persistent force against the superjacent premaxilla.

During the early stages of maxillary sinus osteolysis, the maxilla itself, though increasingly cavitated, retains its integrity ; its lamina compacta withstands the interior expansile strain and pressure atrophy bears upon the more superficial premaxilla only. This therefore thins, atrophies in multiperforate fashion and undergoes absorption, leaving the subjacent maxilla locally exposed as an incisive fossa "ossicle" circumscribed by a "suture". (The formation of a "suture" is characteristic of the facial bones following trauma and other morbid conditions). The pneumolytic process may, by the animal's death, be arrested at this stage, the macerated skull then manifesting "ossicles" in the incisive fossae (Fig. 3).

In the later stages of the process the exposed "ossicular" maxillary surface itself begins to suffer atrophy and absorption. It thins and at multiple and successive foci absorption converts the "ossicular" surface into a completely cribriform sheet (Figs. 4, 5). Later still, in advanced age, a punctate pattern of focal absorption becomes manifest in the upper (extra-"ossicular") area of the infranarial fossa, both the deeply-placed maxilla and the superficially-disposed premaxilla being jointly absorbed at any particular focus. Such a cribriform transformation of the whole infranarial fossa is the terminal phase in the extended process of maxillary sinus osteolysis.

It is now apparent why infranarial "ossicles" characterise fully adult or oldish skulls of *Loxodonta* and *Elephas* and why in *Loxodonta*, wherein a greater degree of pneumatic osteolysis of the relatively more massive cranium is required, such "ossicles" occur almost twice as frequently as in *Elephas*.

This reduction, in the elephant skull, of a substantial slab of premaxillary

and maxillary bone into a mere osseous lacework, by the agency of the maxillary sinus, has its physiological counterpart among cetaceans: for Fraser & Purves (1958) have reported, for certain cetacean species, a comparable reduction of the pterygoid bone, through the agency of the pterygoid sinus, by cavitation, fenestration or even complete absorption.

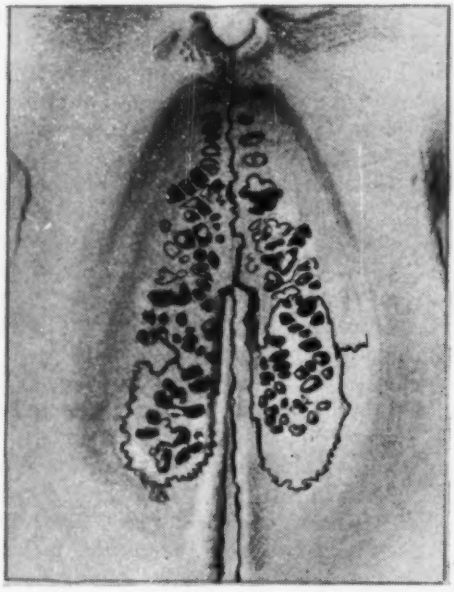

Fig. 5.—*Loxodonta africana* (B.M.49.532). Very old animal. Infranarial region showing cribriform appearance from maxillary sinus osteolysis.

The exact nature of the process whereby the interior architecture of cranial bones may undergo, from expansion of the dominant pneumatic paranasal cavities, a remodelling and transformation so radical as to involve complete removal, remains ill-understood. Such profound bone-changes, however, merely reflect the extreme plasticity of osseous tissue and demonstrate forcefully its perpetual subservience to the different functional demands made upon it. Whatever the particular degree of pneumatisation attained in any topographical instance, its achievement is essentially nothing more than the persistence, in response to overriding physiological requirement, of that inherent capacity for osteolysis manifested by the paranasal sinuses from their initial ontogenetic appearance. Although the intrinsic nature of pneumatic osteolysis remains obscure, its progress and effects are obtrusively apparent. Its fundamental importance in the mechano-physiology of the mammalian cranium—perhaps nowise better exemplified than in the elephant—is so self-evident as not to warrant emphasis.

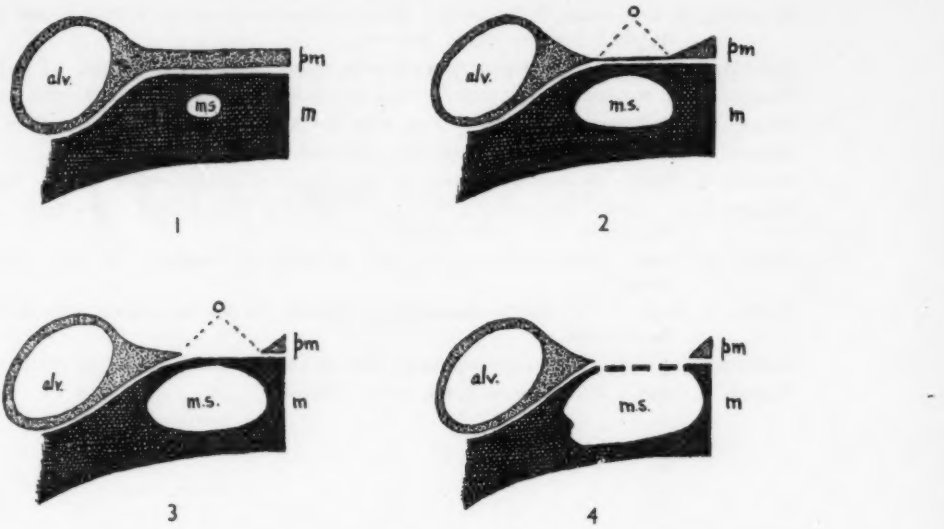

Fig. 6.—Diagrammatic sectional representation of stages in infranarial osteolysis. Stage 1, premaxilla overlies maxilla as harmonic suture ; 2, maxillary sinus enlargement produces atrophy of premaxilla ; 3, further sinus enlargement, disappearance of superjacent premaxilla and "ossicle" formation ; 4, cribriform perforation of exposed maxillary "ossicle". alv=alveolus of tusk (incisor) : max=maxilla, palatine process : m.s.=maxillary sinus : pm=premaxilla : o="ossicle".

ACKNOWLEDGMENTS

Grateful acknowledgment is made to Dr F. C. Fraser, Keeper of Zoology, British Museum (Natural History), for ever-ready access to material in his charge, and to Miss J. E. King and Dr C. J. Porteous for their kind assistance in the examination of specimens. Figs. 2 to 5 are the work of Mr Erik Thorn.

SUMMARY

1. The occurrence is reported of infranarial pseudo-ossicles in mature Asiatic and African elephant skulls.

2. The nature of these formations is shown to result from pneumatic osteolysis.

3. The effects of maxillary sinus enlargement upon maxilla and premaxilla are detailed.

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VERNAL COITION OF THE SEAL *PHOCA VITULINA* IN SHETLAND

BY

U. M. VENABLES AND L. S. V. VENABLES

Ty'n Lon, Bodorgan, Anglesey, N. Wales

[Accepted 14th October 1958]

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INTRODUCTION

The main mating season for the Common Seal (*Phoca vitulina*) in Shetland follows the pupping and moulting seasons and extends from the first week of September to the first week of October (Venables & Venables, 1957). It is accompanied by erotic pair-rolling behaviour in the water. In the final discussion of our paper (*op. cit.* p. 395) we say :—

> " The autumn mating season . . . is not necessarily the only season at which mating can take place. Professor R. J. Harrison (*in lit.*) after histological study of *P. vitulina* from the Wash, has definite evidence of ovulation in May. No blastocysts were found but, taken in conjunction with the high degree of sexual excitement which we have witnessed in May, it suggests the possibility that some matings *may* occur at that season in non-pregnant individuals. Our May observations were carried out in 1953 at the outset of the present study and no sustained watches were kept. Though we failed to see coition at that time [we hardly knew what to look for at this early stage] it is not impossible that occasional coition may take place. Lockley (1954) in his study of *Halichoerus grypus* in Welsh waters describes (pp. 126–28) sexual courtship dances in late February, March, April and early May and, especially in the case of maiden cows and not fully adult bulls, he found this behaviour culminate in coition. The main mating season follows the autumn pupping. "

Backhouse & Hewer (1957) also report spring mating in *Halichoerus grypus* as well as a good deal of homosexual behaviour between males.

In 1958 we revisited this *Phoca vitulina* colony and kept regular daily watches from 23rd May to 10th June, weather permitting. The site of this colony, at the south-west of the Shetland Mainland, has been fully described with a map in Venables & Venables (1955). Weather was favourable practically throughout our 1958 visit : winds were usually light and offshore but visibility was sometimes restricted either by mist or sun glare. For a short period only there was regular early evening disturbance by a lobster boat.

POPULATION NUMBERS

The size of this colony had decreased somewhat. Our highest count of *P. vitulina* was 274 on 25th May 1958 compared with 428 on 26th August 1956. This latter count was taken after the end of the pupping season and included the live pups of the season, whereas in 1958 not a single pup had arrived even at the end of our visit. Pregnant females were plentiful throughout the colony (*e.g.* 10th June : of 128 Common Seals a minimum of 25 were obviously pregnant females). Such females did not keep apart from the other seals except in choosing small, sea-girt rocks for hauling out.

Between 30th May and 9th June (pupping begins *ca.* 14th June), when observation conditions were suitable, we counted the seals near to us, differentiating the yearlings from all other age groups. The seals, of course, may swim from bay to bay within the area and our counts were taken at whichever part of the coastline we happened to be at that time. Eventually the whole area was covered more than once though never all on one day.

On amalgamating the counts it was found that 6·4 per cent were yearlings. At the similar season of 1954 we considered that *ca.* 15 per cent were yearlings and that the number of pups born that year was *ca.* 18 per cent of the total population (Venables & Venables, 1955). However, from 1955 onwards the price of pups' pelts has risen from 30 to 50 shillings and this has more than doubled the annual kill of pups at this colony (Venables & Venables, 1957).

Our highest count of *Halichoerus grypus* in the area was 135 on 26th May but this seemed to be a temporary peak and their numbers had fallen to less than a hundred by 3rd June. The two species sometimes quarrelled for positions on hauling-out rocks but practically ignored each other in the water, though on one occasion (4th June) we noted some underwater play-chasing by a Common and a Grey Seal : both sub-adult. Throughout our whole visit we saw periodic rolling by " pairs " of Grey Seals, and sometimes one of them had an extruded penis. Little time was spent in watching these couples but, judging by the colour criteria for sexing this species (Hewer & Backhouse, 1959), each couple consisted of one of each sex.

MAY–JUNE COITION

It may be said at once that occasional mating does occur in *Phoca vitulina* at this season but it is certainly rare by contrast with the main mating season in autumn. We probably saw it six times, and definitely once, during our visit. As actual insertion takes place below the sea surface it is difficult to see clearly and usually must be largely inferred from the position, immobility and general behaviour of the pair.

There were frequent outbursts of sex play during this pre-pupping season. They seemed unconnected with any conditions of time and tide : three or four pairs would be performing in one part of the area while another area was quiet, and vice versa. Since more seals are in the sea towards high water this in itself is conducive to more aquatic play. That this rolling behaviour was sexual and that actual *pairs* were concerned seems likely from the fact that the penis was frequently extruded in *one* member of the pair and that this individual usually made sporadic attempts to mount his partner. Indeed

a great deal of the rolling performance can be interpreted as effort on the part of the male to control and mount an unwilling female. Much less preliminary play occurs in the autumn mating when the females are more willing. Rolling is fully described in Venables & Venables (1957).

However, these unwilling females took enthusiastic part in the rolling and bubble-blowing pursuit behaviour, sometimes for two or three hours on end. This bubbling is a common, *though not invariable*, part of the behaviour in both sexes. If the seal sinks tail first it blows a gentle bubble-chain beginning soon after sinking, and it almost always rises close on the tail of the bubbles. If it sinks head first, or diagonally, it either blows a brief, more violent, bubble-chain or fails to blow at all. Both members of the pair, on separate occasions, have also been seen to slap the water with their flippers or wave sea-weed (or even driftwood) in the air.

Solitary individuals may go through some or all of these antics, sometimes continuing alone for long periods or, in other cases, being joined by a second individual as if the antics acted as an invitation. Very rarely a change of rolling partners was seen, whereas we never witnessed this during the main autumn mating season. Also a single seal might join a rolling pair and make a three-roll group (which in itself sometimes led to a change of partner), or two rolling pairs would join into a four-roll group resulting in hopeless confusion for the seal-watchers! These interruptions often broke up the behaviour pattern altogether or prevented a promising attempt at mating.

When the rolling behaviour led towards actual mounting so that the male, often with penis already extruded, was in a favourable position for insertion, the female almost always arched her head and neck backwards and so prevented him from getting far enough forward for insertion, or even slipped him right off her back altogether. This back-arching often became a backward somersault and so led to further rolling. On occasions the back-arching would be accompanied by a bite directed at the male's head and neck, much like the nipping of necks indulged in by pairs in the early stages of rolling. Probably some real biting occurs for several individuals were seen with fresh neck wounds on nape, side and throat. The majority of these wounded seals were not yet fully grown.

Clearly the females were unwilling, perhaps physically unready, to pair at this season. This raises the question, " What age-groups are involved in this performance? " Most full-grown cows were already heavily pregnant and due to begin pupping in mid-June. They fished or lay quiescent on tidal rocks and never took part in any form of play. Nor did we see any yearlings taking part, so most of the females involved were probably maiden cows approaching their first oestrus and not yet eager for coition. No yearling males took part and full-sized bulls only seldom, so this behaviour was chiefly confined to the intermediate age-groups (*i.e.* two or three-year olds).

Coition, in the rare instances when it occurred, lasted about two minutes and involved no repeated flextures. Two quotations from our field notes illustrate the type of behaviour witnessed and the difficulty of certainty of

observation. In the first case coition actually succeeded whereas in the second case only exceptional visibility showed that no insertion occurred.

> "*June 5th.* (*Calm water, brilliant sun*). 10.16 *a.m.* Pair of vitulina begin to roll on and below surface. Some round and round underwater chasing. At 10.37 penis extruded. Constant attempts to mount but female back-arched him off. Penis quite soon retracted. Then mostly underwater round and round play-chasing and some ordinary rolling. At 10.50 penis extruded again and female now willing. Mounted awash in clear water over a weedless rock. Few exploratory pelvic thrusts and then final insertion as they sank. No further pelvic thrusts. Remained mounted about two minutes and floated apart as they surfaced. Then floating-bottle attitude a few feet to a few yards apart : rolling not resumed so unable to see retraction of penis. They began to fish (?) soon after 11.00 and we lost them."
>
> "*June 3rd.* (*Flat calm, bright sunshine*). 9.50 a.m. . . . with one of these two rolling pairs the male developed an extruded penis. Quickly mounted female while awash. Was on her four minutes awash and below surface (very clear shallow water) but, by back-arching her head from time to time she never let him get far enough forward for insertion. After four minutes she rolled him off sideways and his penis quickly retracted during a little gentle rolling. Then underwater chasing, during which we lost them in *Laminaria*."

Probable coition was witnessed on our first full day of observation (23rd May). The last coition actually seen was on 5th June but active sexual rolling continued right to the end of our observations (10th June).

MOUSA

This is an uninhabited island of about 450 acres situated on Lat. 60°N. off the east coast of Shetland Mainland. We visited the isle on 25th May 1958 and found a colony of 175 *Phoca vitulina* at very suitable pupping terrain on the east side. Some hauled-out females were heavily pregnant and during our short stay we witnessed typical rolling behaviour from several pairs in the water and one probable coition.

All wild life on Mousa is protected as far as is possible by the laird, Robert Bruce of Sandlodge, but the presence of a remarkably preserved Pictish Broch entails a number of visitors each summer.

DISCUSSION

The discovery of occasional May–June mating in *Phoca vitulina*, together with Professor R. J. Harrison's histological evidence of ovulation in May, suggests that a few cows might well become pregnant at this season. As yet we have no definite evidence of any such early pregnancy. Harrison found no May blastocysts and we ourselves saw no early pups during the summers of 1953, 1954 and 1958.

Our present observations show that young males actively seek coition during May and June whereas most young females are definitely unwilling. The prolonged riding behaviour and, more particularly, the occasional successful mating may well act as a stimulus to ovulation. In such circumstances, if the ovum is actually fertilized, it seems probable that implantation of the blastocyst must be delayed until the normal season. Birth would then occur in the normal pupping season.

Neal's observations on the Badger (*Meles meles*) showed two mating periods : February–May and July–September. As pairing is usually more prolonged in spring, and as most animals have blastocysts by June, he now concludes (Neal,

1958) that the spring mating, after pupping, is the normal one and implantation is normally delayed until December : nearly *ten* months. Secondary oestrus in July–September may, exceptionally, result in fertilization with a much *reduced* period of delay.

In *Phoca vitulina* it appears that the main mating period (September–October) is likewise after pupping. Exceptional matings, in non-pregnant females, may perhaps succeed in May–June, with an *extended* period of delay. In this seal the normal season for implantation is probably " before January but after 1st November " : (Professor R. J. Harrison, personal communication).

ACKNOWLEDGMENTS

Our gratitude is due to the Nature Conservancy who once again defrayed the expenses of our expedition. Dr L. Harrison Matthews read the manuscript of this paper.

SUMMARY

1. A colony of *Phoca vitulina* was under regular observation from 23rd May to 10th June 1958. Outbursts of sexual rolling were common between sub-adult pairs. No yearlings and no pregnant females took part, and fully grown bulls did so rarely.

2. Both sexes rolled enthusiastically. Changes of partner were rare. Many males appeared eager for coition but the females, by arching back their heads and necks, usually prevented them from getting far enough forward for insertion. Successful coition was witnessed on at least one, possibly six, occasion(s).

3. Probably rolling females were maiden cows, approaching oestrus. Ovulation can occur in May and may well be stimulated by this prolonged riding behaviour.

4. The main mating season (September–October in Shetland) follows lactation and moult. In our three years' experience of this colony all pups were born during the three weeks commencing 14th June. If successful fertilization occurs in May, the implantation of the blastocyst is probably delayed until the normal season.

5. A recent decline in the size of this seal colony may be due to the increase in price offered for pups' pelts with a consequent increase in hunting.

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NOTES AND ABSTRACTS

MEETINGS OF THE SOCIETY FOR SCIENTIFIC BUSINESS

10th February 1959

Mr J. N. Ritchie, C.B., B.Sc., F.R.C.V.S., in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : DECEMBER, 1958 AND JANUARY, 1959

By L. Harrison Matthews, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the months of December 1958 and January 1959 were 182 in number, including some domestic animals. The following are of special interest : a White-crown Mangabey *Cercocebus torquatus lunulatus*, presented by Mrs R. W. Reed ; two Guinea Baboons *Papio papio*, presented by Mr J. W. Woodward ; a collection of animals brought from Paraguay by Mr David Attenborough and presented by the British Broadcasting Corporation, Television Service, including an Azara's Douroucouli *Aotes trivirgatus azarae* (Humboldt), new to the collection, a Maned Wolf *Chrysocyon brachyurus*, four Paraguayan Ring-tailed Coatis *Nasua nasua aricana* Vieira, four different species of Armadillo—the Nine-banded *Dasypus novemcinctus*, Seven-banded *Dasypus septemcinctus* ; Six-banded *Euphractus sexcinctus* and La Plata Three-banded *Tolypeutes matacus*. Among the birds were two Maximilian's Parrots *Pionus maximiliani*, a Crested Cariama *Cariama cristata* and four White-crested Guans, *Pipile jacutinga*, included among the reptiles were two St. Hilaire's Terrapins *Hydraspis hilarii* and a Great Tegu *Tupinambis teguixin* ; a Raccoon-like Dog *Nyctereutes procyonoides*, presented by Dr K. C. Searle, C.M.Z.S.; a White-fronted Capuchin *Cebus albifrons*, presented by Mr L. Hamilton-Renwick ; a Geoffroy's Tamarin *Oedipomidas spixi*, presented by Mr A. T. Campbell ; two Ring-tailed Lemurs *Lemur catta*, presented by Mr J. A. Looker ; a Gentoo Penguin *Pygoscelis papua*, received in exchange ; two Ganges Soft-shelled Turtles *Torionyx punctatus*, received in exchange and a Gaboon Viper *Bitis gabonica* and two Nose-horned Vipers *Bitis nasicornis*, born in the Menagerie. During the same period there were 163 additions to the Menagerie at Whipsnade Park, apart from transfers from London.

The following communications were read and discussed :—

The Earl of Cranbrook, C.B.E. Poisonous saliva of the Water Shrew

Neomys fodiens bicolor. (Illustrated by a film). [Summary of a paper to be published in the ' Proceedings ']

Mr R. N. T.-W.-Fiennes and Mr O. Graham-Jones. Studies of a nutritional disease (Osteodystrophia fibrosa) of young lions, associated with changes of the skeleton and symptoms of muscular weakness. [To be published in the ' Proceedings ']

Dr W. Lane-Petter. Film of the Japanese Monkey Centre.

10th March 1958

N. D. Riley, Esq., C.B.E., Vice-President, in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : FEBRUARY 1959

By L. Harrison Matthews, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the month of February 1959 were 43 in number, including some domestic animals. The following are of special interest : two Slender Lorises *Loris tardigradus*, purchased ; four Long-nosed Bandicoots *Perameles nasuta*, presented by Dr A. G. Lyne ; and a Siamese Fire-backed Pheasant *Diardigallus diardi*, received in exchange. During the same period there were 12 additions to the Menagerie at Whipsnade Park.

The following communications were read and discussed :—

Dr W. C. Osman Hill. Remarks on the newly discovered Golden Langur of N.W. Assam.

The series of coloured photographs exhibited were taken by Mr E. P. Gee, Assam, of the Golden Langur *Presbytis* (*Trachypithecus*) *geei* recently discovered by him on the Sankosh River in N.W. Assam.

Reports of the existence of a new species of monkey had been received from planters over some ten years, but in November 1953 Mr Gee visited the area and filmed the animal. Several troops were observed comprising twelve or more individuals, one troop even had thirty to forty members.

The photographs showed a male of the new species alongside one of the commoner Capped Langurs *Trachypithecus pileatus* indicating the differences between them. In the new form the crown hairs do not form a mat and show no differentiation from the temporal hairs. The general colour dorsally is whitish or creamy (mixed with some black on the crown) ; the hands and feet whitish ; throat orange-red, this tinge ascending to the cheeks, sides of neck and downwards to the chest. An ill-defined half-whorl occurs on the forehead—not present in the Capped Langur. Males are larger than females and have the orange more extensive (covering the whole ventral surface). There is some evidence of a seasonal change of pelage, the golden tinge being more evident in cold weather.

Specimens have been collected and described by Khajuria of the Calcutta Museum and of these a topotype has been donated to the British Museum.

This Langur ranges over a quadrangular territory in Goalpara south of the Bhutan border, north of the Brahmaputra and limited on the west by the Sankosh River. From correspondence with Mr Gee, it now transpires that it occurs also in the Garo Hills, south of the Brahmaputra where *T. pileatus* also occurs. This strongly suggests complete speciation, i.e. *T. geei* is not merely a local race of *T. pileatus* as the speaker had formerly believed.

The golden element in the pelage, I suggest, may possibly be explained as a retained infantile feature insofar as newly-born infants of all the known forms of the subgenus *Trachypithecus* are uniformly golden in colour, undergoing typically a postnatal change to grey or black. The newborn of *T. geei* is said to be almost white.

References : Gee, E. P., 1955. *J. Bombay nat. Hist. Soc.* **53,** 252–254.
Khajuria, H., 1956. *Ann. Mag. Nat. Hist.* (12) **9,** 86–88.

Mr JOHN BUNYAN. The effect of hypochlorite on animal tissues. (Illustrated by a film).

Dr E. H. ASHTON and Dr H. G. VEVERS. The number of exhibits, births and deaths in the Menagerie at Regent's Park 1835–1957 and in Whipsnade Park 1931–1957. [To be published in the ' Proceedings '].

Dr PETER CROWCROFT. Small mammals of the Channel Islands.

14th April 1959

Sir LANDSBOROUGH THOMSON, C.B., O.B.E., D.Sc.,
President, in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : MARCH 1959

By L. HARRISON MATTHEWS, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the month of March 1959 were 104 in number, including some domestic animals. The following are of special interest : a Pale Capuchin *Cebus apella pallidus* Gray, new to the collection, purchased ; two Cotton-headed Tamarins *Oedipomidas oedipus*, presented by Mr C. J. Allen ; a male Jaguar *Panthera onca*, originally deposited, later purchased ; four Squirrel-like Flying Phalangers *Petaurus norfolcensis*, six Short-headed Flying Phalangers *Petaurus breviceps*, and two Spotted-tailed Dasyures *Dasyurus maculatus*, presented by Sir Edward Hallstrom to commemorate the visit to Taronga Park, Sydney of the Rt. Hon. Harold Macmillan ; a Red-and-Yellow Barbet *Trachyphonus erythrocephalus* Cabanis, new to the collection, presented by Mr P. H. Maxwell ; a consignment of reptiles and amphibians from the Bahamas, including the following which are new to the collection—a Cat Island Water Tortoise *Pseudemys felis* Chapman, two Lion Ameiva *Ameiva thoracica* Cope and a

Bahaman Brown Snake *Alsophis vudii* Cope, presented by Mr W. A. King-Webster ; two Bahaman Brown Snakes *Alsophis vudii* Cope, presented by Mr McNeir Brown and a Greenhouse Frog *Eleutherdactylus ricordii* Dumeril & Bibron, presented by Mr Peter Wormwood. During the same period there were nine additions to the Menagerie at Whipsnade Park.

The following communications were read and discussed :—

Dr W. H. Thorpe. Talking birds and the mode of action of the vocal apparatus of birds. [To be published in the ' Proceedings '].

Professor A. J. E. Cave. Pneumatic osteolysis in the elephant skull. [To be published in the ' Proceedings '].

Mr. H. N. Southern and Mr Oliver Hook. Management of large mammals in East Africa. (Illustrated by a film).

NOTICE

["Proceedings", Vol. 132 Part 3, was published on the 29th May 1959.]

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